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THE IN VIVO INCORPORATION OF C^{14} FORMATE IN THE UREIDE GROUPS OF URIC ACID BY PERIPLANETA AMERICANA (L.)[1]

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INTRODUCTION

Leifert (1939) postulated the formation of the ureide carbons of uric acid in insects by a condensation of 2 moles of urea and one of a dicarboxylic three carbon acid; this synthesis was based on the pathway first suggested by Wiener (1902). Brighenti and Colla (1940) found no increase of uric acid in the silkworm after the injection of urea and concluded that urea was not involved in the synthesis of uric acid by insects. Furthermore, labeled urea was not incorporated to a significant extent into the purine ring by vertebrates (Barnes and Schoenheimer, 1943). The use of labeled formate has demonstrated in vertebrates and yeast that formate is incorporated into carbons 2 and 8 of the purine ring (Buchanan, 1951).

To determine the role of formate in the formation of the ureide carbons of uric acid by the roach, labeled formate was injected, the uric acid of the fat body was isolated, identified, and degraded; and the activity of the carbons of the purine ring established.

MATERIALS AND METHODS

Adult female roaches, *Periplaneta americana* (L.), from a strain reared on dogfood were used throughout this work. All roaches were placed on a fishmeal diet, 60% protein, three days prior to the injection of the formate and held on this diet during the experimental period. This fishmeal diet was used during the experimental period to insure a high rate of uric acid formation in the presence of the injected formate. Haydak (1953) showed that the roach, on high protein diet, accumulated a uric acid-like substance (positive murexide test) in the fat body.

A 0.059 M solution of sodium formate (2) with an activity of 0.1 μc. per μl. was injected with a Dutky-Fest microinjector through the ventral membranous area immediately anterior to the proximal end of the metathoracic subcoxa. Three days after the last injection the fat bodies were removed and the uric acid extracted with an 80° C. solution of 0.1% Li_2CO_3. The resulting solution was filtered and the uric acid was crystallized in the cold after acidification with 10% HCl. The isolated material was washed with a 1: 1 mixture of ethyl alcohol and diethyl ether and then with ice cold water. This material was recrystallized three times and gave a white crystalline material. Uric acid isolated by this method from a mixture of control fat body and labeled formate was free of radioactive contamination. The uric acid was identified by a comparison of its absorption spectrum in the region of 255–300 mμ with a known sample of recrystallized uric acid and by following the decrease of its absorption peak at 291 mμ under the specific action of uricase (Kalckar, 1947).

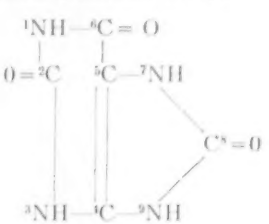

FIGURE 1. Uric Acid.

The conventional numbering system shown in Figure 1 has been used to designate the positions of the carbon atoms in the uric acid molecule. Carbons 2 and 8, representing the ureide carbons of the pyrimidine and imidazole rings of uric acid, respectively, may be separated from each other by appropriate degradation procedures. An alkaline MnO_2 oxidation (Buchanan *et al.*, 1948) separated carbons 6 and mixed 2 and 8. A chlorine oxidation (Sonne *et al.*, 1948) yielded carbons 2, 8, and mixed 4, 5, and 6. The activity

[1]Paper of the journal series, New Jersey Agriculture Experiment Station, Rutgers University, The State University of New Jersey. Accepted for publication Dec. 7, 1956.

of mixed carbons 4 and 5 was determined by the difference.

The CO_2 from the degradation of uric acid was trapped in 1.0 N NaOH and precipitated as $BaCO_3$ following the procedure of Comar (1955). The $BaCO_3$ was recovered as a plate with a Tracerlab precipitator on a dried tared filter paper. The plate was dried over alumina for 24 hours, weighed, and counted with a mica end window G. M. Tube. The activity of the $BaCO_3$ was determined from a correction curve prepared from $BaCO_3$ plates made in a similar manner from a calibrated standard solution of $Na_2C^{14}O_3$.[2]

The oxidation of the injected formate was followed by the collection of the respiratory CO_2 in 1.0 N NaOH throughout the experimental period. Immediately after injection the roaches were placed in a metabolism cage and CO_2-free air was drawn through the cage continuously. The respiratory CO_2 was trapped in 1.0 N NaOH and at intervals the Na_2CO_3 was collected and $BaCO_3$ plates prepared in a manner similar to that used in the uric acid degradation study. All counts of these plates were made at infinite thickness and the activity determined by plates prepared from a standard solution of Na_2CO_3.[2]

The average value of the uric acid content of the fat body of female roaches was determined by the removal of the fat bodies and extraction of the uric acid with 0.1% $LiCO_3$. This uric acid content was determined by a modified Folin colorimetric test (Kern and Stransky, 1937) with a Beckman DU spectrophotometer.

RESULTS

The results of the degradation of the fat body uric acid are given in Table I. The appearance of active carbons in positions 2 and 8 indicates that they can be formed from the same source, a one-carbon unit at the same oxidation level as formate.

The average uric acid content of the fat bodies of 20 female roaches was 12.7 ± 3.9 mg. of uric acid. Using this same value for the injected animals, approximately 3% to 5% of the injected activity was recovered in the uric acid of both experimental groups.

The activity in the respiratory CO_2 from 12 female roaches, each injected with 1.0 μc. formate, is shown in Table II. These results show a rapid decline in the rate of $C^{14}O_2$ production. Fifteen hours after injection, 19.6% of the original formate activity appears in the respiratory CO_2. As a constant rate of $C^{14}O_2$ production occurs in the 15 to 34 hour time period, the oxidation of conversion products is indicated.

The fecal material was collected for four days following injection and in the water soluble fraction of this material, a total of 0.037 μc. of activity was found. As this is 0.3% of the original injected formate activity, excretion of unchanged formate does not occur to any appreciable extent and thus is not a factor in the rapid decrease of $C^{14}O_2$.

TABLE I

ACTIVITY OF URIC ACID CARBONS[a]

EXPERIMENT NUMBER[b]	TOTAL C^{14} FORMATE PER ROACH	URIC ACID CARBON NUMBER				
		2	4, 5[c]	6	4, 5, 6	8
	dis./min.	dis./min./μM Carbon				
1[d]	66 x 10^5	1437 ± 28	123 ± 14	21 ± 3	89 ± 9	1923 ± 30
2[e]	111 x 10^5	2317 ± 32			167 ± 18	3307 ± 43

[a]Uric acid recovered three days after last injection.
[b]Eight female roaches used in each experiment.
[c]Determined by difference.
[d]Single injection.
[e]First injection 37 x 10^5 dis./min., followed by a three day interval, second injection 74 x 10^5 dis./min.

TABLE II

ACTIVITY IN RESPIRATORY CO_2[a]

TIME (HOURS)	ACTIVITY μC. PER HOUR	% OF TOTAL INJECTED ACTIVITY
0–3	0.317	7.9
3–6	0.218	5.5
6–9	0.127	3.2
9–12	0.092	2.3
12–15	0.026	0.7
15–27	0.013	1.3
27–39	0.012	1.1

[a]12 adult female roaches each injected with 1.0 μc. formate.

DISCUSSION

The activity found in carbons 2 and 8 of uric acid indicates that the ureide carbons can be formed from a single carbon source at the oxidation level of formate. In the avian system purine carbon 8 is incorporated by the addition of a formyl group to glycine amino ribotide; purine carbon 2 is incorporated by the addition

[2]Tracerlab, Boston 10, Massachusetts.

of a formyl group into 5-amino-4-imidazolecarboxamide ribotide (Warren and Flaks, 1956). This incorporation of a formyl group is a general transformylation in which the beta-carbon of serine can serve as the donor with "folic acid" as a necessary cofactor (Sakami, 1955). It is probable that the same type of transformylase system operates in the roach to introduce the C^{14} of formate into the ureide carbons. In the original work with pigeons (Sonn *et al.*, 1948) a ratio of 1: 1 of C^{13} for carbons 2 and 8 was found in the uric acid. It is felt that the ratios of C^{14} found in the roach, 1: 1.3 and 1: 1.4 for carbon 2 and 8, shows a real difference. A possible explanation based on the different role of uric acid can be formulated. In the pigeon the uric acid is excreted as formed and there is no storage system analogous to the urate cells of the insect fat body. If the stored uric acid serves as a nitrogen depot as suggested by Ludwig (1954), it would be expected to be in a state of dynamic equilibrium. Reversable cleavage of the purine ring at position 2 would lead to loss of activity at this position by exchange with unlabeled formate during the latter part of the holding period. Thus, after the original *de novo* synthesis of the uric acid in the presence of labeled formate in the first fifteen hours, the activity in position 2 could be reduced by an exchange of formate at this position during the remainder of the holding period. The addition of carbon 2 and closure of the purine ring by formation of inosinic acid has been shown to be a reversible process (Buchanan *et al.*, 1955).

The rapid decrease in the rate of $C^{14}O_2$ production in the first fifteen hour period indicates that formate rapidly becomes unavailable for oxidation. The formate is not removed by excretion as no significant amount of activity was found in the water soluble fraction of the feces. In addition, the activity in the fat body uric acid accounted for only 3% to 5% of the injected activity. Thus the major portion of the injected formate must be incorporated into urates not located in the fat body or into other metabolic pathways.

A transformylase system, capable of incorporation of one-carbon units into many compounds in addition to the purines, has been found in vertebrates. The synthesis of serine from glycine by the addition of a formyl group in the β position of serine may play a central role in transformylation as the formation of serine functions in the collection, storage, and distribution of single carbon units (Sakami, 1955).

It was suspected that the formation of serine in the roach could account for the metabolic fate of the formate as a pool of free glycine has been demonstrated in roach blood (Pratt, 1950). Preliminary *in vitro* work with fat body has shown the formation of labeled serine from C^{14} formate. Further work is in progress on the location of the C^{14} in the labeled serine and the effect of a folic acid-free diet on the incorporation of formate.

SUMMARY

When injected into the roach, C^{14} formate is incorporated into the ureide carbons of the uric acid recovered from the fat body. After injection of labeled formate, activity appears in the respiratory CO_2 and declines rapidly in the first fifteen hours. No significant amount of formate is found in the excreta following injection.

It is postulated that a transformylase system similar to that found in other organisms accounts for the metabolism of formate in the roach.

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CONTRIBUTIONS TO THE MORPHOLOGY AND PHYLOGENY OF THE REDUVIOIDEA (HEMIPTERA: HETEROPTERA).

PART I. THE MORPHOLOGY OF THE ABDOMEN AND GENITALIA OF PHYMATIDAE[1]

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INTRODUCTION

The superfamily Reduvioidea was established by Reuter (1910) who placed it with the Cimicoidea and Aradoidea in the series Anonychia. Later (1912) he added the Tingoidea to Anonychia and removed from it the Aradoidea. Leston, Pendergrast and Southwood (1954), favoring the practice of basing the nomenclature of higher categories on generic names, have designated a group more or less equivalent to Reuter's Anonychia as Cimicomorpha. These authors place the remainder of the terrestrial Heteroptera in a second group, the Pentatamorpha.

The families orginally placed in the Reduvioidea by Reuter (1910) were Reduviidae, Phymatidae, Enicocephalidae, and Nabidae. In the years since this classification was proposed inclusion of various other families has been suggested. However, these additions were not generally accepted and in 1943, Usinger included only the original four families in his revised classification of the Reduvioidea. Even in more recent years the classification of this superfamily has remained unsettled. Carayon (1950a) has shown that the Nabidae, exclusive of the subfamily Pachynominae, are related to the Anthocoridae and, therefore, this family is now placed with the anthocorids in the Cimicoidea. At the same time Carayon transfered the Pachynominae to the family Reduviidae, but subsequently (1954) concluded that they represent a distinct family, the Pachynomidae. Elasmodemidae, which was formerly a subfamily of Aradidae, has been raised to the rank of family by Wygodzinsky (1944) who places it in Reduvioidea, and China (1955) has returned Joppeicidae to the Reduvioidea where it had earlier been placed by Reuter (1912). In summary then, the families now assigned to the Reduvioidea are Reduviidae, Phymatidae, Pachynomidae, Enicocephalidae, Joppeicidae, and Elasmodemidae.

The systematic position of a few families of the Cimicomorpha such as the Tingidae is not well established and, therefore, the possibility of their belonging to the Reduvioidea must be considered. The Tingidae along with the Piesmidae constituted the superfamily Tingoidea (Reuter, 1912) but since various authors have shown these families are unrelated, the superfamily has a questionable status. A relationship of tingids to reduviids is suggested by the work of Leston, *et al.* (1954) who indicate that the wing venation of these families is similar, and by China (1955) who places the Tingidae adjacent to the Reduviidae in his revised family tree. However, Carayon (1954) asserts that the tingids have characteristics of both reduviids on one hand and mirids (Cimicoidea) on the other. Kormilev (1955) has recently described a new family, Vianaididae, which he considers to be related to the Tingidae; further study of this family may provide additional evidence regarding the affinities of the tingids.

In addition to the Tingidae other families have been reported to have both cimicoid and reduvioid characteristics. Drake and Slater (1957) have concluded that the Thaumastocoridae belong to the Cimicoidea but indicate that they have certain reduvioid characteristics. Similarly, China (1955) although placing the Joppeicidae in the Reduvioidea notes that they have several cimicoid characteristics. Leston, in fact, on the basis of wing venation includes them in the Cimicoidea (Leston, *et al.*, 1954) and Drake and Slater (1957) note that the hind wing venation of the cimicoid thaumastocorids is identical to that of the joppeicids. Carayon (1954) points out that the female genitalia of joppeicids resemble those of tingids, indicating a possible relationship between these two. Clearly the significance of the occurence of both reduvioid and cimicoid characteristics in these families indicates a need of much additional study.

The evidence for the inclusion in the Reduvioidea of at least two of the six families listed above is not conclusive. As we have noted, the Joppeicidae have both cimicoid and reduvioid characteristics and, therefore, there is no general agreement regarding their systematic position. The Enicocephalidae which were only tentatively placed in the Reduvioidea by Reuter (1910) have since been shown to have certain very unique features which cast considerable doubt about the propriety of their present systematic position

[1]Accepted for publication December 18, 1956.

(Carayon 1950b; Leston *et al.*, 1954). Of the remaining reduvioid families the affinities of the Phymatidae and Elasmodemidae to the Reduviidae are reasonably well established while those of the Pachynomidae are somewhat less so. However, the precise details of their relationships in terms of specific subfamilies involved deserves much additional study.

Limitations comparable to those discussed above are encountered in our knowledge of the reduvioids on the subfamily level, especially in the family Reduviidae. Here the subfamilies are very diverse and their relationships quite complex and in many instances very obscure (see Usinger, 1943). There are at present approximately thirty reduviid subfamilies, considerably more than in any other family of Heteroptera. Because of the large number and diversity of these subfamilies there arises a need to reconsider the status of many of these groups with the possibility in mind that some may be combined while others may merit family status. However, it is strongly felt that any major changes made in the reduvioid family and subfamily arrangements should be based on a thorough study of the entire group. Nothing is to be gained by the indiscriminate raising of subfamilies to family rank or by the creation of additional subfamilies on the basis of seemingly minor differences.

In addition to the inherent complexity of the relationships of the Reduvioidea the study of their phylogeny is made very difficult by the extreme rareness of many forms. Since they are distributed primarily in tropical areas inacessible to many workers, new species and genera as well as an occasional annectant form are still being described. Furthermore, as a result of the scarcity and inaccessible distribution of many forms, very little evidence of relationships can be obtained at present from ecological, behavioral, cytological, and physiological studies and we are therefore limited mostly to the study of gross morphological features. Fortunately this limitation is not serious since experience has shown that, in general, evidences of animal relationships gained from these other areas of study have only tended to confirm earlier conclusions based on morphological studies.

However, it is quite important that the phylogeny be based on as many structural characteristics as can be made available. For this reason, detailed and comprehensive morphological studies are especially essential for the solution of the many problems involved in the phylogeny of the Reduvioidea. In particular, investigations of the morphology of the male and female genitalia appear to offer great promise since in the various other groups of insects in which they have been studied extensively, the genitalia have generally proven to be a good source of characters of value in demonstrating affinities at various systematic levels. Although there have been studies of a few reduvioids, information regarding the morphology of the genitalia of most subfamilies is lacking.

Therefore, this projected series of studies has been undertaken in which the genitalia and related abdominal structures of the various families and subfamilies of the Reduvioidea will be investigated on a detailed comparative basis. In the first paper of the series the family Phymatidae is considered. Our knowledge of the genitalia of this family is based primarily on the descriptions by Handlirsch (1897) of features visible externally, and descriptions of the phallus by Singh-Pruthi (1924) and Kormilev (1951).

MATERIAL STUDIED

The family Phymatidae consists of three subfamilies, Phymatinae, Macrocephalinae, and Carcinocorinae (Handlirsch, 1897). A species representing each of these subfamilies has been selected for study. *Phymata pennsylvanica* Handlirsch is used as a representative of the Phymatinae.[2] Since this is a rather common neartic species and fresh specimens could be easily obtained, it was possible to study its internal reproductive organs as well as cuticular structures of the genitalia. For a comparison of the variation within this subfamily a neotropical species, *Phymata fortificata* (Herrich-Schaeffer) was also studied. This species and *Phymata pennsylvanica* represent different subgenera of the single genus recognized in the subfamily (Kormilev, 1951).

The subfamily Macrocephalinae is represented by *Macrocephalus tuberosus* Westwood, a neotropical species. The subfamily Carcinocorinae is represented by *Carcinocoris castetsi* Handlirsch which was collected in southern India. Although only dried specimens of these last two species were available, it was found that the major abdominal muscles could be suitably studied after soaking the material in hot water for a short period of time.

MORPHOLOGICAL DESCRIPTIONS

The Abdomen

As in other Heteroptera, the tergum is the only portion of the first abdominal segment that is clearly distinguishable and in phymatids the first and second terga are fused (fig. 1, *Tg 1*). Segments two through nine are quite distinct but the tenth and eleventh segments are considerably reduced and are sexually dimorphic. Therefore, these latter segments will be described more fully in the sections devoted to the male and female genitalia.

[2]Kormilev (1953) has recently concluded that *Phymata pennsylvanica pennsylvanica* Handlirsch and *Phymata pennsylvanica americana* Melin are distinct species, and that *Phymata pennsylvanica coloradensis* Melin is a subspecies of the latter. Therefore we now have *Phymata pennsylvanica* Handlirsch, *Phymata americana americana* Melin, and *Phymata americana coloradensis* Melin.

In each species studied except *Carcinocoris castelsi* there is a line of flexibility extending midventrally through the pregenital segments (figs. 2, 4, *a*). In the female of *Carcinocoris* the situation is somewhat different. Membranous areas extend obliquely through each segment differentiating the sternopleura into lateral sclerites and a median triangular sclerite (fig. 3).

The abdomen of phymatids is generally characterized by the pronounced development of the connexiva as, for example, may be seen in figure 2 (*Cnx*). However the macrocephalines usually do not have especially prominent connexiva (fig. 4, *Cnx*) although in a few species such as *Macrocephalus productus* Barber they are well developed.

In the phymatids the connexiva extend as a continuous rim across the end of the abdomen (fig. 1, *Cnx*). In this respect they are different from many other heteropterans in which the connexiva are less clearly differentiated or entirely lacking on the posterior abdominal segments. In the female phymatid the connexivum extends transversely through the eighth tergum (*Tg 8*) and, therefore, the posterior half of this tergum (fig. 2, *Tg 8*) and the succeeding abdominal segments are shifted to a ventral position on the abdomen. In the male there is a corresponding modification of the connexivum but the connexivum extends through the seventh tergum (fig. 5, *Tg 7*).

The connexiva are distinctly delimited by dorsal and ventral connexival sutures (fig. 1, *dCS*, fig. 2, *vCS*). The ventral connexival suture of *Macrocephalus* is represented by a strip of convoluted membrane (fig. 4, *vCM*) which may be considerably stretched as the abdomen expands.

The intersegmental membranes of the pregenital segments of phymatids are much reduced, or completely lost. There is a corresponding reduction or loss of the longitudinal intersegmental muscles of these segments. The reduction is least in *Carcinocoris* in which intersegmental membranes and muscles are present on the venter but very poorly developed.

In *Macrocephalus* the pregenital intersegmental membranes and muscles are completely lacking except between the sternopleura of segments two and three (fig. 4). The second sternopleural sclerite is rather firmly united with the metathorax. Therefore, movements which occur between the thorax and abdomen are made possible by membranes between the thorax and first abdominal tergite dorsally and between the second and third sternopleurites ventrally.

Pregenital segmental membranes are entirely lacking in *Phymata* and there is a corresponding loss of intersegmental muscles except for those between the thorax and abdomen. Membranes between the thorax and abdomen allow the latter to bend slightly.

The first pair of abdominal spiracles of phymatids are located dorsal to the connexiva on protuberances on the first abdominal tergite (fig. 1, *Sp 1*). The remaining abdominal spiracles lie just mesad of the ventral connexival sutures on the second through seventh abdominal segments (figs. 2, 4, *Sp 2*). In the female there is also a pair of spiracles on the eighth abdominal segment in the ventral connexival suture (fig. 3, *Sp 8*). These spiracles appear to be considerably reduced. In the male the eighth segment is much reduced and the spiracles are concealed (fig. 5, *Smt 8*).

Vestiges of the nymphal scent gland openings may be seen near the posterior margin of tergites four and five (fig. 1, *StG*).

The Female Genitalia

The external genitalia of female phymatids are greatly reduced and certain parts are apparently lost entirely. To facilitate an understanding of these modifications a brief description of the generalized structure of the female genitalia of Heteroptera is necessary. This discussion will also serve to present the terminology used in this paper. For a more detailed treatment of the terminology of both male and female genitalia of Heteroptera the reader should refer to the recent paper of Dupuis (1955).

The supporting base of the external genitalia of heteropterans consists of pairs of sclerites, the *first* and *second gonocoxopodites* (valvifers). Extending from each sclerite are processes which are

Abbreviations Used In the Plates

Als, antlia seminalis
An, anus
Cnx, connexivum
dCS, dorsal connexival suture
Dej, ejaculatory duct
dPlS, dorsal phallic sclerite
Edp, endophallus
FrB, basal foramen
Gap 1, 2, 3, gonapophyses
GCap, genital capsule
GCh, genital chamber
Gcp 1, 2, gonocoxopodites
GM 1-13, genital muscles
Gop, gonopore
IfP, inferior process
Msd, mesadenia
Odc, common oviduct
Odl, lateral oviduct
Ov, ovary
PApd, promotor apodeme
Pl, phallus
Pm, paramere
PrPl, phallic lobe
Pspt, pseudospermatheca
Ptg, proctager
RApd, remotor apodeme
Rct, rectum
Smt 8, segment eight
Sp, spiracle
SpA, suspensory arm
Spt, spermatheca
StG, scent gland scars
Stp, stapes
Str, strut
Tes, testis
Tg, tergum
vCM, ventral connexival membrane
vCS, ventral connexival suture
Vd, vas deferens
Vsm, vesicula seminalis
Vu, vulva

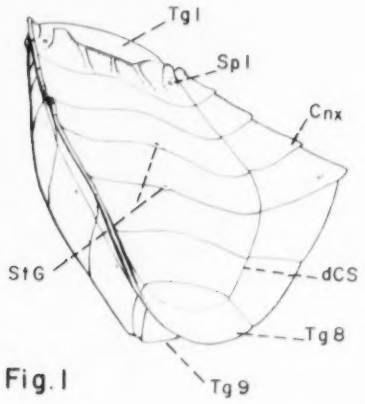

Fig. 1

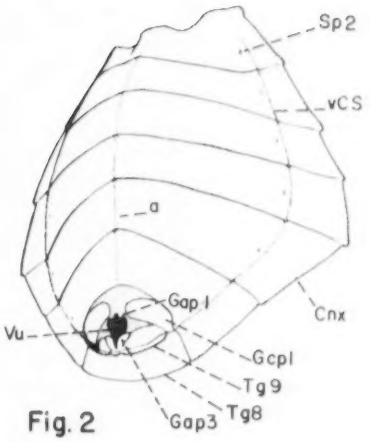

Fig. 2

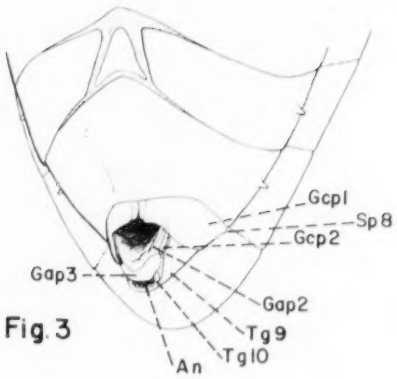

Fig. 3

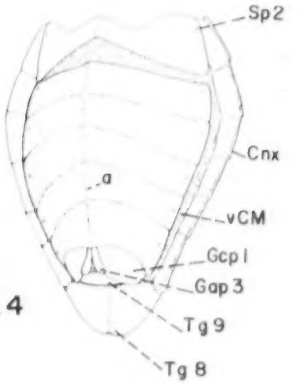

Fig. 4

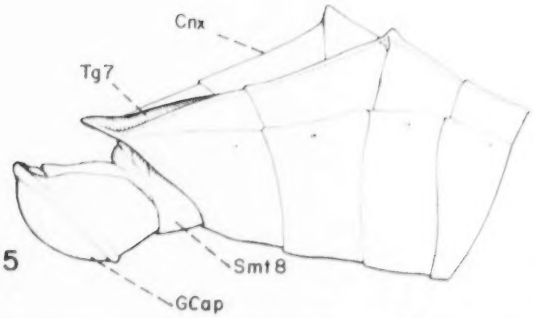

Fig. 5

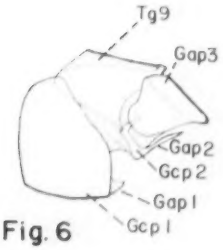

Fig. 6

1. Posterior dorsolateral view of the female abdomen of *Phymata pennsylvanica*.
2. Posterior ventrolateral view of the female abdomen of *Phymata pennsylvanica*.
3. Ventrolateral view of the terminal abdominal segments and female genitalia of *Carcinocoris castetsi*.
4. Ventrolateral view of the female abdomen of *Macrocephalus tuberosus*.
5. Lateral view of the male abdomen of *Phymata pennsylvanica*.
6. Lateral view of the female genitalia of *Macrocephalus tuberosus*.

the *first* and *second gonapophyses* (valvulae) and these together constitute the ovipositor. An additional pair of processes, the *third gonapophyses*, extending from the second gonocoxopodites, is often distinguishable in heteropterans. However, these do not serve as ovipositor blades, as they do in certain orthopterans, but sometimes do form part of an ovipositor sheath.

The external female genitalia of phymatids may be most conveniently described in relation to the ninth tergum which is a triangular sclerite lying in an almost vertical plane beneath the posterior margin of the connexivum (fig. 1, *Tg 9*). In relaxed specimens the apex of this sclerite may be drawn backwards as shown in fig. 2, exposing the genitalia more fully. In this position two distinct lobe-like sclerites may be seen on each side of the apex of the ninth tergum (figs. 2, 4, *Gap 3*). These are the third gonapophyses. In *Carcinocoris* the third gonapophyses are fused into a single piece (fig. 3, *Gap 3*).

The anal opening lies between the apex of the ninth tergum and the third gonapophyses (fig. 3, *An*). In *Carcinocoris* the tenth segment is a small sclerite arching over the anal opening (fig. 3, *Tg 10*). In the other species studied the tenth segment is not distinguishable. The remnants of the eleventh segment are probably represented by small, indistinctly sclerotized areas forming the margin of the anus.

Anterior to the lateral inflected margins of the ninth tergum there is a pair of elongated sclerites articulated dorsally to the connexivum of the eighth segment (fig. 2, *Gcp 1*). These sclerites are the first gonocoxopodites. Extending posteriorly from the mid-ventral membrane joining the gonocoxopodites, there is a pair of small, distinct lobes (fig. 2, *Gap 1*). These are interpreted as being the vestiges of the first gonapophyses.

In *Macrocephalus* a small L-shaped sclerite is articulated to the lateral margins of the ninth tergum (fig. 6). The basal portion of this sclerite represents the second gonocoxopodite (*Gcp 2*). The apical portion is free and represents the second gonapophyses (*Gap 2*). In *Carcinocoris* the second gonocoxopodites are more reduced but may be recognized as small sclerites characteristically articulated to the margins of the ninth tergum (fig. 3, *Gcp 2*). The second gonapophyses are apparently represented by a thin sclerotized strip extending posteriorly from each gonocoxopodite (*Gap 2*). However, these are not free but lie in the body wall. In *Phymata* the second gonocoxopodites and their apophyses are so reduced that they are virtually indistinguishable.

The external genitalia surround the broad external opening of the genital chamber (fig. 2, *Vu*). When viewed dorsally the genital chamber is seen to be more or less quadrate (figs. 7, 11, *GCh*). Extending from near its posterior margin is a long convoluted gland (fig. 11, *Spt*). In specimens that have been treated with KOH only the cuticular intima is seen (fig. 7, *Spt*). This gland is homologous to the spermatheca of other insects but instead of receiving spermatozoa it has been modified to function as a colleterial gland. When the genitalia are opened out during oviposition, the roof of the genital chamber is drawn downward, so that the opening of this gland is near the substratum onto which the secretion is released. The relatively large size of this gland appears to be correlated with the fact that phymatids deposit their eggs in a mass bound together by liberal amounts of egg cement.

A pair of tubular organs extend from near the anterior edge of the genital chamber (fig. 8, *Pspt*). These organs have a cuticular intima which may be seen in KOH-treated specimens (fig. 7, *Pspt*). They serve to receive and store spermatozoa but are not homologous to the usual spermatheca of other insects. They are, therefore, termed *pseudospermathecae* (Carayon, '54). In *Phymata* pseudospermathecae are rather short and s-shaped. In *Carcinocoris* and *Macrocephalus* the organs are long, thin, and convoluted and near their apices they terminate in a small sclerotized bulb (figs. 9, 10, *Pspt*). Between the pseudospermathecae the common oviduct extends from the genital chamber (fig. 7, *Odc*).

The female genitalia of *Phymata fortificata* and *P. pennsylvanica* have essentially the same characteristics.

The description of the remainder of the female genital tract and muscles of phymatids is based on a study of the fresh and preserved specimens of *Phymata pennsylvanica* only.

The common oviduct (fig. 11, *OdC*) is joined to the ovaries by short lateral oviducts (*OdL*). The ovaries each consist of three ovarioles containing eggs in various stages of development (*Ov*).

Three sets of muscles are inserted on the genital chamber. The first are paired longitudinal muscles which originate near the anterior margin of the seventh sternopleuron and are inserted on the lateral edges of the genital chamber (fig. 11, *GM 1*). Next, paired transverse muscles originate on the first gonocoxopodites and are inserted on the dorsal and ventral walls of the genital chamber (*GM 2*). The third pair originates laterally on the ninth tergum and is inserted on the posterior wall of the genital chamber (*GM 3*). The primary function of these muscles is probably to move the egg through the genital chamber during oviposition.

If the genital chamber is carefully dissected away as shown in Fig. 8, then the remainder of the genital muscles may be seen. A pair of muscles originates midlaterally on the seventh sternopleuron and is inserted on the anterior margin of the first gonocoxopodites (*GM 4*). These muscles serve to draw the gonocoxopodites

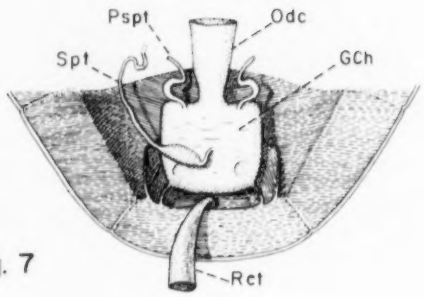

Fig. 7

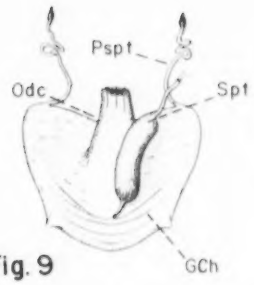

Fig. 9

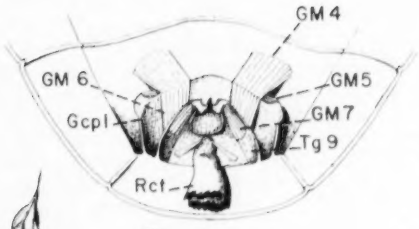

Fig. 8

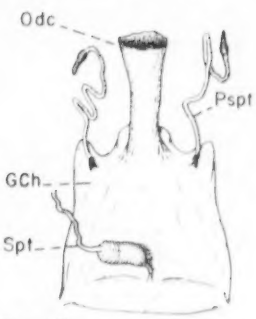

Fig. 10

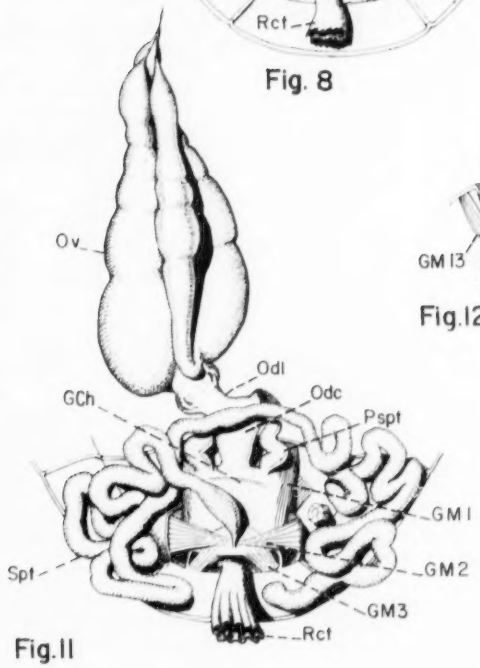

Fig. 11

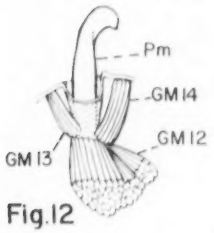

Fig. 12

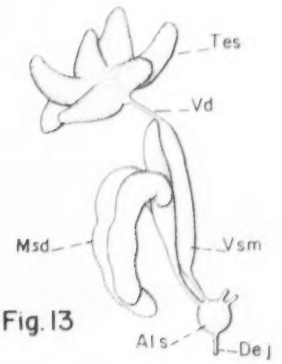

Fig. 13

7. Dorsal view of the internal female genitalia of *Phymata pennsylvanica*.

8. Dorsal view of the posterior ventral abdominal wall of the female of *Phymata pennsylvanica*, showing genital muscles.

9. Dorsal view of the genital chamber of *Carcinocoris castetsi*.

10. Dorsal view of the genital chamber of *Macrocephalus tuberosus*.

11. Dorsal view of the reproductive system of *Phymata pennsylvanica*.

12. Lateral view of the musculature of a phymatid paramere.

13. Male reproductive organs of *Phymata pennsylvanica*.

inward. A second pair of muscles originates on the seventh sternum beneath the first gonocoxopodites and is inserted on the upper angles of the gonocoxopodites (*GM 5*). These muscles serve to pull the gonocoxopodites outward into the position shown in figure 2

Paired muscles originating on the anterior margins of the first gonocoxopodites are inserted on the inflected lateral portions of the ninth tergum (fig. 8, *GM 6*) and are the retractor muscles of the ninth tergum. On the lateral portions of the ninth tergum there originates a pair of muscles which is inserted on the third gonapophyses (*GM 7*). In this dissection a small pair of rectal muscles originating on the ninth tergum may also be seen.

The structure of the genitalia of *Macrocephalus* and *Carcinocoris* indicates that they have essentially the same genital musculature as *Phymata*. In addition, they probably also have small muscles associated with the second gonocoxopodites.

The Male Genitalia

As in the section devoted to the female genitalia, a brief presentation of the morphology of the generalized male genitalia of Heteroptera will be given to introduce the terminology and to aid in the understanding of the genitalia of phymatids. The venter of the ninth segment of Heteroptera is a bulbous sclerite termed the *genital capsule* (pygophore). The body wall behind the genital capsule is invaginated into the latter forming the *atrium genitale*, a chamber which contains the intromittent organ, or *phallus*. At the base of the phallus there is a typically stirrup-shaped sclerite, the *stapes* (basal plates), by which the phallus is articulated to the exoskeleton of the genital capsule. Between the arms of the stapes there is an orifice, the *foramen basal* through which the *ductus ejaculatorius* passes from the general body cavity into the phallus. The arms of the stapes are generally joined above the basal foramen by a sclerotized piece, the *ponticulus basilaris*. The phallus of heteropterans is typically differentiated into a proximal portion, the *phallosoma*, and a distal portion, the *endosoma*. In repose the endosoma is usually telescoped into the phallosoma. Arising from near the base of the phallus is a pair of genital claspers, the *parameres*.[3] These appendages extend from the genital atrium and at rest lie folded along the margin of the genital capsule.

In phymatids the genital capsule and eighth segment are ordinarily withdrawn into the seventh segment so that only a small portion of each is exposed. When the bug mates, these segments are, by means of body fluid pressure, extended posteriorly as shown in figure 5. In this position the entire genital capsule (*GCap*) and eighth segment (*Smt 8*) may be seen. The eighth segment is greatly reduced, the tergum being entirely membranous. The spiracles are embedded anteriorly in the tergal membrane beneath the connexivum. These spiracles are probably functional only when the eighth segment is extended since they are otherwise completely covered.

The dorsum of the ninth segment forms a very weakly sclerotized roof over the genital capsule (fig. 14, *Tg 9*). At the posterior margin of the roof of the genital capsule the body wall turns inward as a broad flat tube, the *proctiger*, (*Ptg*) within which lies the anus. This broad tube probably represents the tenth and elventh segments. To defecate the tube is everted so that the anus is extended beyond the rim of the genital capsule.

At rest the parameres of phymatids lie folded just inside the posterior margin of the genital capsule (fig. 14, *Pm*). They arise from the wall of the genital atrium but retain their primitive attachment to the base of the phallus by means of a very tenuous ligament. The adjacent margins of the genital capsule serve as fulcra for the movements of the parameres. Because of this relationship the parameres may appear to be directly articulated to the margin of the genital capsule.

From its posterior edge the genital capsule extends inward forming a broad floor beneath the parameres (fig. 15, *IfP*). In Phymata this region is flat and simple. However, in *Macrocephalus* and *Carcinocoris* it is differentiated into median and lateral lobes (figs. 16, 17, *IfP*). This structure has been termed the *inferior process* (Singh-Pruthi, 1925). The lateral lobes of the inferior process probably serve as additional fulcral surfaces for the parameres.

Beneath the base of each paramere the exoskeleton of the genital capsule extends inward in the membranous wall of the genital atrium (fig. 15, *SpA*). These processes are known as the *suspensory arms* of the phallus. At their apices the suspensory arms are articulated to large tuberosities at the end of each branch of the stapes (fig. 18, *PvAt*) and this articulation serves as the pivot for the erectile and retractile movements of the phallus.

Above the pivotal articulation a pair of apodemes, terminating in a large disk, extends from the stapes (fig. 18, *PApd*). These are the *promotor apodemes* of the phallus. Just below each pivotal articulation is found the tendon-like *remotor apodeme* of the phallus (fig. 18, *RApd*).

The phalli of the species studied are considerably different from one another in appearance. However, they do have many important structural features in common. The most dis-

[3]Although the designation of heteropteran claspers as *gonostyli* was tentatively adopted by the author in a previous paper, it is now felt that this term is unsuitable since the homologies indicated by it probably do not exist. Therefore *paramere*, the older and more generally used term, is considered to be more suitable.

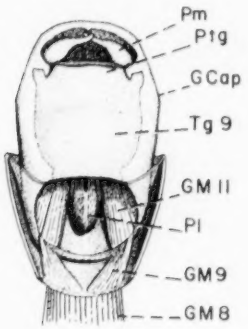

Fig.14

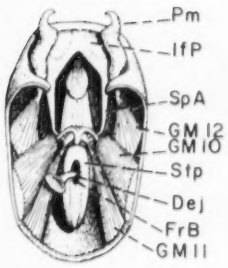

Fig.15

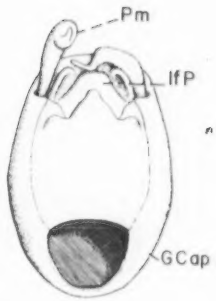

Fig.17

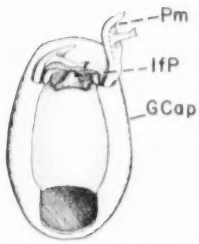

Fig.16

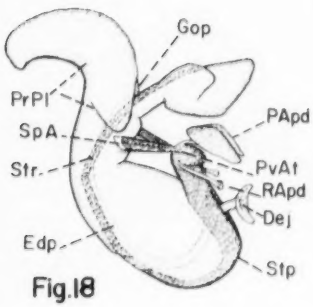

Fig.18

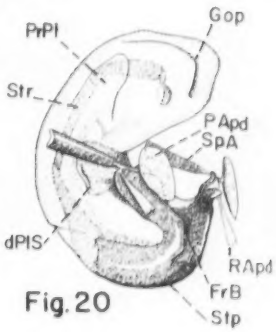

Fig. 20

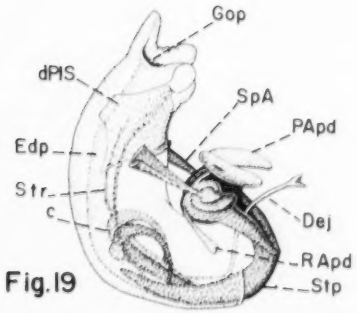

Fig.19

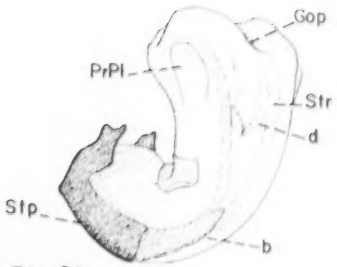

Fig. 21

14. Dorsal view of the genital capsule of *Phymata pennsylvanica*.
15. Dorsal view of the male genitalia and musculature of *Phymata pennsylvanica*.
16. Dorsal view of the genital capsule of *Macrocephalus tuberosus* showing the right paramere extended.
17. Dorsal view of the genital capsule of *Carcinocoris castetsi* showing the left paramere extended.
18. Lateral view of the expanded phallus of *Phymata pennsylvanica*.
19. Lateral view of the phallus of *Macrocephalus tuberosus*.
20. Dorsolateral view of the phallus of *Carcinocoris castetsi*.
21. Ventrolateral view of the phallus of *Carcinocoris castetsi*.

tinctive feature is lack of differentiation of the phallus into a phallosoma and endosoma and that the phallus consists primarily of the phallosoma.

At the base of the phallus there is found a well differentiated stapes (fig. 20, *Stp*). In *Carcinocoris* and *Macrocephalus* the stapes is of the usual stirrup shape characteristic of heteropterans. In *Phymata*, however, the arms of the stapes are not joined by a sclerotized arch extending below the basal foramen. Therefore, the arms are joined only above the basal foramen by the *ponticulus basilaris*, and the stapes is more the shape of an inverted *U* (fig. 15, *Stp*).

In each species the basal portion of the stapes is prolonged in an arc onto the ventral surface of the phallus (fig. 18). This ventral prolongation is forked, and the distal portion of it extends into the inside of the phallus (fig. 21, *b*). In *Phymata* and *Carcinocoris* the internal extensions of the stapes are joined to long, thin sclerites termed *struts* (figs. 18, 21, *Str*). The struts extend internally through the phallus to its apex. In *Macrocephalus tuberosus* struts may be distinguished but are less well developed (fig. 19, *Str*). Also in this species there is an unusual complex of sclerites lying between the internal extensions of the stapes (fig. 19, *c*). Similar sclerites have been described in other species of *Macrocephalus* (Kormilev, 1951) and may be characteristic of this genus or of its subfamily.

The ejaculatory duct, after passing into the phallus through the basal foramen, proceeds ventrally to the proximal ends of the struts (fig. 18, *Dej*). Here the ejaculatory duct joins a wider duct, the endophallus (*Edp*) which extends between the struts through the remainder of the phallus to an external opening, the *gonopore* (*Gop*). The struts lie in the lateral walls of the endophallus from which they appear to have been derived rather than from the stapes. The peculiar sclerites in *Macrocephalus*, which were described above, also lie in the wall of the endophallus. In *Carcinocoris* there is also a complex of sclerites in the wall of the endophallus but these are located more distally than those in *Macrocephalus* (fig. 21, *d*).

On the dorsal surface of the phallus of *Carcinocoris* and *Macrocephalus* there is a large distinct sclerite (figs. 19, 20, *dPlS*). This sclerite is not found in *Phymata*. Near the end of the phallus of *Carcinocoris* there are expansible lateral lobes (fig. 21, *PrPl*). Dorsal and ventral expansible lobes are found at the end of the phallus of *Phymata* (fig. 18, *PrPl*). These lobes probably serve to help hold the phallus in the female genital chamber during copulation.

The male genitalia of *Phymata fortificata* have essentially the same characteristics as those of *P. pennsylvanica*.

The ejaculatory duct of *Phymata* originates in a bulbous structure, the *antlia seminalis* (seminal pump) (fig. 13, *Als*). Anteriorly two pairs of ducts enter the seminal pump. Each of the mesal pair leads from an elongate, tubular *vesicula seminalis* (*Vsm*) which in turn is joined to the testis by a short *vas deferens* (*Vd*). Each testis (*Tes*) consists of seven testicular tubules which extend freely in various directions rather than being bound together by a peritoneal sheath as is the case in many insects.

Each of the lateral pair of ducts entering the seminal pump leads from an elongate bladder-like portion of the *mesadenia* (accessory gland) (fig. 12, *Msd*). This portion of the gland lies appressed to the seminal vesicle and receives the secretion of an appended pair of glandular lobes.

In *Phymata* pairs of ventral intersegmental muscles extend between the seventh and eighth segments (fig. 14, *GM 8*) and between the eighth segment and the genital capsule (*GM 9*). These muscles act in two ways. First they serve to draw the genital capsule into the abdomen in the resting position. Their second action occurs when the genital capsule and eighth segment are extended posteriorly. This extension occurs as a result of an increase in body fluid pressure and unilateral contraction of the intersegmental muscles results in a bending and rotation of the genital capsule to the left or right.

The phallus of *Phymata pennsylvanica* is provided with pairs of promotor and remotor muscles. The promotor muscles originate anteriorly on each side of the genital capsule and are inserted on the promotor apodemes of the phallus (fig. 15, *GM 10*). The remotor muscles originate on the genital capsule just below the promotors and are inserted on the remotor apodemes of the phallus (*GM 11*). The antagonistic action of these two pairs of muscles results in pivotal movements of the phallus on the articulations at its base. By means of these movements the apical portion of the phallus may be extended dorsally out of, or withdrawn ventrally into, the genital capsule.

Three muscles are associated with each paramere. The most prominent of these extends anteriorly from its insertion on the paramere to its origin on the side of the genital capsule (fig. 12, *GM 12*). The other two are smaller muscles which extend posteriorly from their insertion on the paramere to their origin on the posterior portion of the genital capsule (*GM 13*, & *14*).

DISCUSSION

Morphological Considerations

The significance of the structure of the phymatid abdomen may be best appreciated when contrasted to the structure of the generalized abdomen of the Heteroptera. Of the various families of this suborder the segmentation of the abdomen is, in most respects, more generalized in such families as Saldidae, Miridae, and Nabidae. In these families the connexiva are not especially prominent and the intersegmental muscles and intersegmental membranes of the

abdomen are not reduced. Their abdomen, like that of the more generalized insects, increases in volume by a telescopic extension of the segments and to some extent by a dorsal-ventral expansion. In other families of Heteroptera such as the Reduviidae, Lygaeidae, and Pentatomidae there are various degrees of reduction of the intersegmental muscles and membranes of the abdomen. As a result of this reduction, the abdomen becomes limited mostly to dorsal-ventral expansion, and various modifications which facilitate this type of expansion are found. In particular the connexiva are frequently well developed since they act as hinges which enable the dorsal and ventral abdominal surfaces to move together or apart.

In the phymatids the abdominal expansion is of the dorsoventral type. However, in *Carcinocoris* ventral intersegmental muscles and membranes are present although considerably reduced. In this particular respect *Carcinocoris* is the most primitive of the phymatids studied. Also we may conclude that the heteropterans from which the phymatids arose possessed intersegmental abdominal muscles since it is not likely that these muscles would have been lost and then reappeared in the Carcinocorinae.

In *Macrocephalus* there is a special modification of the connexivum which facilitates dorsoventral expansion. This modification is a convoluted membrane found where the ventral connexival suture would normally occur. The stretching of this membrane allows the underside of the abdomen to expand ventrad. Most abdominal expansion must occur in this direction since the top of the abdomen is almost entirely covered by the broad, flat, rigid scutellum. This means of abdominal expansion eliminates the need of the connexiva as a hinge mechanism. It is therefore not suprising to find that the connexiva are typically not prominent in the Macrocephalinae.

The lack of differentiation of the phymatid phallus into phallosoma and endosoma raises the question of whether this lack indicates a primitive condition or is the result of a secondary loss of the endosoma. The evidence clearly favors the latter alternative. The undoubtedly primitive hemipteran phallus of most Auchenorrhyncha is characterized not only by its lack of differentiation into phallosoma and endosoma but by the fact that the paired basal plates are not fused to form a stapes and by the intimate association of the parameres with the phallus. In phymatids the stapes is, of course, well formed, and the parameres have become secondarily associated with the genital capsule. Furthermore, the entire phymatid phallus corresponds in general to the phallosoma of the reduviid phallus. Therefore, it seems reasonable to conclude that the structure of the phymatid phallus represents a quite specialized condition resulting from the loss of the endosoma. This loss may possibly be correlated with the reduction of the ovipositor and ventrad shift of the genital opening of the female since, as a result of these modifications, the phallus does not need to extend so far to reach the genital chamber.

Similar modifications of the phallus are found in reduviids of the genus *Metapterus* and mirids of the subfamily Phylinae. Since these groups are not particularly related to the phymatids it is probable that the loss of the endosoma has occured independently in at least a few instances in the Cimicomorpha. China (1955) has noted that the phallus of gelastocorids, pelogonids, and joppeicids is undifferentiated and he places great importance on this feature as one indicative of a very primitive condition. However, it would seem that the lack of an endosoma can not in itself be taken as an indication of a primitive condition but that other primitive features, such as are found in the Auchenorrhyncha phallus, must also be demonstrated.

Subfamily and Family Relationships

Several of the features of the genitalia of the species studied suggest that the Carcinocorinae and the Macrocephalinae are more closely allied to one another than they are to the Phymatinae. In the species representing the first two of these subfamilies it was found that the external genitalia of the female are similar and are more generalized than the genitalia of the phymatines. Also, the pseudospermathecae of the Macrocephalinae are very similar to those of the Carcinocorinae.

In the case of the males the inferior processes of the genital capsule of the carcinocorines and macrocephalines are similar and very different from that of the phymatines. Furthermore, the phallus of the carcinocorines possesses certain characteristics in common with that of the macrocephalines such as a dorsal sclerite on the phallobase and a complex of internal sclerites. These structures are not found in the phymatine phallus, which is also different from the others in having struts which extend beyond the gonopore. It seems likely that the simplicity of the phymatine phallus indicates that it has undergone reduction and may therefore be less generalized than the phallus of the carcinocorines or macrocephalines. However, too little is known at present of the morphology of the reduvioid phallus to be able to ascertain the characteristics indicative of a generalized condition.

The phallus of phymatids, especially that of the carcinocorines and macrocephalines, possesses characteristics which should be very useful in specific and generic determinations.

Until the abdomen and genitalia of the diverse reduviids have been described in more detail, only limited comparisons of these parts of reduviids to those of phymatids can be made. However, these comparisons will be useful in

indicating ways in which the two families may be similar or dissimilar and in suggesting a number of details which in particular should be investigated in the reduviids.

With regard to the general structure of the abdomen of phymatids and reduviids it should be noted that in both families the abdominal expansion is primarily of the dorsoventral type and that there is a corresponding reduction of segmentation. It will be of interest to determine if intersegmental abdominal muscles are present in any reduviids. The extension of the connexivum transversely through the seventh or eighth tergum and the resulting ventrad shift of the terminal abdominal segments which we have noted in phymatids also occurs in varying degrees in many reduviids. The general morphology of the abdomen of the Elasmodemidae as described by Wygodzinsky (1944) is essentially the same as that of phymatids.

The first abdominal spiracles of phymatids lie within the first median abdominal tergite. In some reduviids (Harpactocorinae) they are located in a similar position while in others (Stenopodinae) they are found in the membrane between the abdomen and metanotum. The concealment of the eighth abdominal spiracles of the male is apparently characteristic of phymatids. In many reduviids these spiracles are normally visable externally.

Judging from the descriptions of Villiers (1948), the female genitalia of reduviids are generally less reduced than those of phymatids. In both of these families the third gonapophyses are relatively well developed while in many other heteropterous families they are almost indistinguishable. Wygodzinsky (1944) has reported that only the anterior gonapophyses occur in the Elasmodemidae. These structures have been reinvestigated in connection with the present work and it is felt that they are, in fact, the third rather than the first gonapophyses. If they were the first gonapophyses one would expect them to be articulated to the first gonocoxopodites (eighth sternites of Wygodzinsky). However, they are instead articulated by means of small sclerites (second gonocoxopodites?) to the lateral margins of the ninth tergum in the same manner as the third gonapophyses of phymatids and many reduviids.

The true spermatheca of reduviids like that of phymatids probably has lost its original function and now serves as an egg cement gland. In so far as is known the function of sperm storage has been taken over by the pseudospermathecae (Carayon, 1954). Wygodzinsky (1944) indicates that these organs are also found in elasmodemids. In reduviids the pseudospermathecae are generally joined to the common oviduct while in phymatids they are joined to the genital chamber.

The phallus of phymatids is best characterized by the reduction of the endosoma and the pronounced ventral extension of the stapes. In general the phallus, especially that of Phymata, resembles most the phallus of the holoptilines (Reduviidae) and the Elasmodemidae as described by Villiers (1948) and Wygodzinsky (1944), respectively. The seminal pump of phymatids is a median bulbous organ located at the junction of the vasa deferentia and ejaculatory duct. It is rather similar to the seminal pump of cimicids (Davis, 1956). In those reduviids that have been studied it has been found (Carayon, 1944, 1950) that, instead of a bulbous seminal pump at the beginning of the ejaculatory duct, there is typically a pair of small, elongate sacs. Carayon (1950) has reported that similar structures are found in phymatids but the present study is not in agreement with this observation. On the contrary, it appears that the seminal pump of phymatids may be distinctly different from the corresponding structure characteristic of many reduviids.

Dr. James A. Slater (University of Connecticut) has given many helpful suggestions in the preparation of this paper, and he and N. A. Kormilev (Buenos Aires, Argentina) have generously provided many of the specimens studied. Their assistance is gratefully acknowledged. I am also indebted to J. C. Lutz of Philadelphia for the identification of the specimens of *C. castetsi*.

SUMMARY

The phymatid abdomen is characterized by well developed connexiva or connexival membranes and by a corresponding reduction of the intersegmental membranes and muscles. These modifications facilitate dorsoventral abdominal expansion and eliminate the telescopic expansion characteristic of more generalized insects. The segmentation of the abdomen is least reduced in Carcinocorinae.

The connexivium extends transversely through the eighth tergum of the female and the seventh of the male, forming a continuous rim along the sides and across the end of the abdomen. This modification results in a shift of the terminal abdominal segments to a posterior ventral position on the abdomen.

The eighth abdominal spiracles are concealed in the male.

The parts of the external genitalia of the female are greatly reduced except for the first gonocoxopodites and the third gonapophyses. The genitalia of phymatines are more reduced than those of carcinocorines and macrocephalines.

A pair of pseudospermathecae opening into the genital chamber of the female receive and store the spermatozoa. The true spermatheca is well developed but functions only as a colleterial gland.

The genital capsule of the male is much like

that of other heteropterans. The parameres appear to be articulated to the genital capsule but actually arise from the wall of the genital atrium near the base of the phallus. The phallus is articulated in the genital atrium by suspensory arms from the genital capsule.

The most distinctive feature of the phallus is the lack of an endosoma. The stapes is characteristically prolonged onto the ventral surface of the phallus where it passes inward to join the struts. The struts appear to be derived from the endophallus. There are various expansible lobes on the phallus which serve to anchor the organ during copulation.

At the junction of the vasa deferentia and ejaculatory duct there is a bulbous organ similar to that of cimicids.

The male and female reproductive organs and genital musculature of *P. pennsylvanica* are described.

The structure of the female genitalia, the pseudospermatheca, the genital capsule, and the phallus indicates that the Carcinocorinae and Macrocephalinae are more closely allied to one another than they are to Phymatinae.

The modifications of the abdominal segmentation of phymatids are similar to those found in reduviids and Elasmodemidae. In these families the females are characterized by the well developed third gonapophyses, by having pseudospermathecae, and by having a colleterial spermatheca. The males of each family have a similar stapes and their phallus is supported by struts.

The phymatids differ from most reduviids in the following respects: the female genitalia are more reduced, and in the male the eighth spiracles are concealed, the endosoma is reduced, and the seminal pump is bilobed.

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PRINCIPLES OF ZOOLOGY, by JOHN A. MOORE. 1957. Oxford University Press, New York, N. Y. 696 pp. $7.50.

This text is one of the best in the field of general zoology that I have had the pleasure of reading, studying and reviewing. The author, in my estimation, has done an excellent job in the preparation of this text to fulfill his aims of "teaching zoology and teaching science". In the preface he states that "superficial treatment of a wide variety of topics must be sacrificed for a meaningful consideration of a few". However in developing these few topics he utilizes pertinent information from many different fields. In this way one is able to develop and understand certain basic facts and principles which in turn lead to sounder inferences and conclusions regarding the major biological concepts.

I should like to emphasize that all portions of this text are well written and well illustrated. The author has made it an easy book to read, to study and to use as a reference. By this I am not implying that he has oversimplified, but rather that he has good organization, good language use and good summarizations.

Finally, the author has written this text in an interesting, informative, and stimulating manner without resorting to teleology. It is obvious that he enjoyed writing this book and undoubtedly enjoys teaching.

W. C. MYSER.

OVIPOSITION RESPONSE OF THE IMAGO OF THE CORN EARWORM, HELIOTHIS ZEA (BODDIE), TO VARIOUS WAVE LENGTHS OF LIGHT[1,2]

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INTRODUCTION

Continued work on the response of *Heliothis zea* to various wave lengths of light was suggested by preliminary work on the effects of various preferred host plants and non-preferred plants as a stimulus to oviposition. It was thought that the presence of host plants in oviposition cages of *Heliothis zea* might stimulate the females to a higher percentage of copulation and egg deposition. Originally two cages approximately 2 feet square were set up with no host plant in one cage and fresh ears of corn, in silk, in the other cage. The cage with corn contained 12 pairs of imagoes and the cage without corn contained 16 pairs. Later, as more imagoes were obtained, the following experiments were set up: A cage with a blooming cotton plant and a cage with a blooming bean plant, both of which are hosts; a cage with a tobacco plant and a cage with a blooming petunia plant, neither of which is normally a host; and a cage with only cloth strips hanging in it. All seven of these cages faced westward toward decreasing crepuscular light intensities, and all were enclosed and had a cloth oviposition surface over the front. Egg counts for the plant and cloth oviposition surfaces in each cage are given in Table I.

The data (Table I) give no indication that moths in cages with plants copulate more or deposit more eggs than those in cages without plants. Since only imagoes that had copulated could deposit fertile eggs and all the eggs were fertile, it was assumed that copulation was about proportional to the eggs laid. The average number of eggs per female was more for the cage with cloth strips than for either cage with cotton or corn silk, both hosts. Only the cage with a host bean plant and one pair of imagoes carried a really higher number of eggs (see Table I.).

The average number of eggs per female for all the imagoes used in the wavelength behavior cage (described below) was 298 compared with an average of 176 for the above cages. No plants were in the behavior cage.

These data definitely show that a cloth surface facing crepuscular light intensities received a greater oviposition response than did host plants. It should be pointed out that eggs on the cloth were far easier to count under a grid than were eggs scattered over a plant; however, assuming that half of the eggs on the plants were missed, the difference between the eggs on the plants (241) and those on the surface facing low intensity light (7341) was great enough to indicate the same conclusion. It should also be noted that in the cage with cloth strips hanging in it, all eggs were deposited on the cloth surface facing the low intensity light.

METHODS

Preliminary experiments had shown that *Heliothis zea* would alight and oviposit on a cloth surface illuminated with crepuscular light in preference to a host plant. This habit of the moth for such surface preference lent itself to light and color experiments, as portions of the spectrum could be projected on the preferred surface and the reproductive and oviposition behavior of the moth observed on the lighted surface. No information is available on the oviposition preference of crepuscular or nocturnal moths for surfaces illuminated with various wavelengths of the spectrum. Furthermore, very little information is available on the response of the crepuscular or nocturnal insects to various intensities of light, such as are found at dusk and by moonlight, nor what the effects of polarized and nonpolarized light are upon the reaction of such insects.

From the physiological standpoint, three physical characteristics of radiation must be considered when attempting to evaluate the effects of visible and near visible radiation on insects or other organisms: (1) the quality of light, that is, wavelength or color; (2) the intensity, energy measured in foot-candles or in gram-calories; and

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[2]A portion of a dissertation presented as a partial fulfillment of the requirements for the degree, Doctor of of Philosophy in Entomology at Kansas State College.

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TABLE 1

EGG COUNTS IN CAGES WITH PREFERRED PLANTS AND NONPREFERRED PLANTS. CAGES ALSO HAD A CLOTH OVIPOSITION SURFACE OVER THE FRONT

CAGE AND PLANTS	TOTAL				
	Number of Pairs Imagoes	Eggs on Plant	Eggs on Cloth	Number of Eggs	Average Eggs per Female
Bean	1	0	620	620	620
Tobacco	2	75	414	489	244
Cloth strips only	1	0	209	209	209
Cotton	9	1	1771	1772	197
No strips or plant	16[a]	—	2601	2601	163
Corn silk	12[a]	165	1478	1643	137
Petunia	2	0	248	248	124
Total eggs	43	241	7341	7582	

[a]Most valid, as largest populations.
Ratio of number of eggs on plant to number on cloth 1 to 30.
Average number of eggs per female 176.

(3) the durations of light, that is, length of time the organism is exposed to the light. Of these three physical characteristics, the second, which involves intensities of radiation, is perhaps most difficult to evaluate and control in any series of experiments on radiation.

A rectangular behavior cage (fig. 1) was designed to test the oviposition response of the imago to competing wavelengths of light. It was 18″ by 18″ by 30″ and designed for an optimum population of from 20 to 30 imagoes. The cage was constructed of ⅝ inch plywood and the whole inside painted with a flat black enamel. On the back wall of the cage was mounted a 7½-watt, red, dark-room bulb with a switch in the circuit. This light could be turned on and off for observation purposes and was low enough in intensity that it did not disturb the activities of the moths. At each end of the cage was cut a pair of six-inch circular holes with tracks on the outside for sliding panels. White cloth was stretched across the panels, which also had six-inch holes cut in them, and could be slipped across the holes in the cage to provide oviposition surfaces for the imagoes. In all the experiments on light and color, only one of each pair of six-inch holes at opposite sides of the cage was used. The other holes were covered with solid panels of fiber board and served as entrances to the cage. They had been cut with the intention of eventually comparing four wavelengths of light at once. The whole front of this cage was covered with a pane of glass which was enclosed in a black observation hood. The hood could be opened or let down around one's head so as to exclude all outside light. That the space requirements of this cage were sufficient is shown by the fact that the percentage of copulation in the cage was as good as,

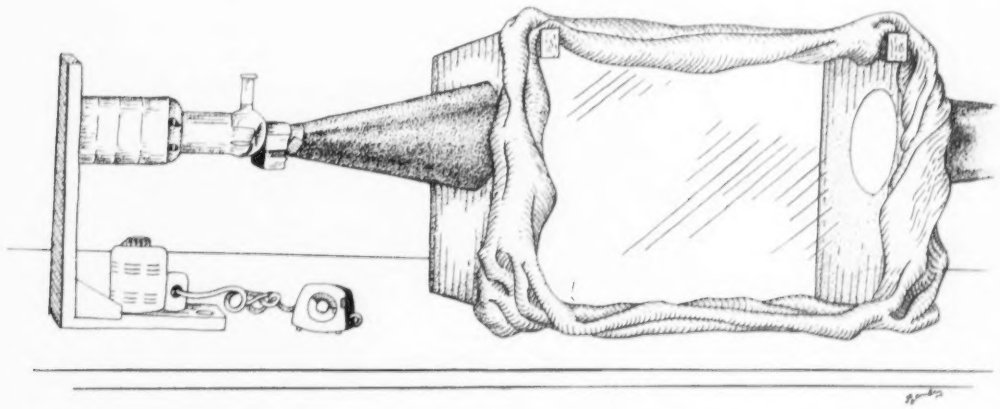

FIG. 1. Apparatus for experiments on competing wavelengths of light. This behavior cage measured 30″ long, 18″ high, and 18″ deep and was designed for observations on a population of 10 or 15 female imagoes paired with males.

or better than, mating recorded from a population collected from a black-light trap[4] in the field.

Two projectors for Polaroid Variable-Color Filters[5] were constructed using 75-watt, reflector-type GE lamps and 250 ml. Florence flasks for condensing lenses. The intensity of the light output from the lamps was controlled by variable powerstatt transformers, type 116, 120 volt input, 0 to 140 volt output.[6] Dark cardboard hoods enclosed the area between the filterholders on the projectors and the circular cloth oviposition windows at each end of the cage. These hoods excluded all extraneous light from the room. When necessary, the projectors were turned on and off by an automatic timer.

Each filter used in these experiments, cut the transmittance of light from its source by certain percentages. Photometric curves supplied with the filters showed transmittance of light values plotted against the wavelength. These values were for the transmittance of polarized light by the variable color filters (selective light-polarizers) alone. Since they were used in conjunction with a neutral polarizer, the percentages of transmittance had to be multiplied by a factor supplied for the filters of 0.38, to obtain the percentage of incident unpolarized light that the two elements transmitted. The percentage of light transmitted at maximum saturation for red, 680 mu, was 0.82 x 0.38 = 31 percent; yellow 580 mu, was 0.86 x 0.38 = 33 percent; green, 530 mu, was 0.28 x 0.38 = 11 percent; and blue, 480 mu, was 0.39 x 0.38 = 15 percent. It can be seen that there were great differences in the amount of light transmittable through the various color filters.

All intensities of light were set with a Weston Master II exposure meter. When the meter light baffle is open, this meter reads on a 0 to 50 candles per square foot scale. The photo cell is directly below the baffle of the meter. This meter proved the most useful as the light sensitive photo cell was approximately the same circumference as the filter, and furthermore this meter gave the intensity readings in candles per square foot and could be read directly on a logarithmic scale. The readings were taken close against the filters and the light source adjusted by varying the voltage with the powerstatt until 1.6 foot-candles was reached. All the experiments were conducted at this intensity (Table II.).

As the percentage of light transmitted decreased with the various filters, the voltage necessary to equalize intensities at 1.6 foot-candles was increased proportionally.

[4]Four-vaned baffle type black light trap which utilized a single G. E. F15T8/BL Lamp. Furnished by the Agricultural Engineering Research Branch, Agricultural Research Station, United States Department of Agriculture, College Station, Texas.

[5]Donated by the Polaroid Corporation, Cambridge, Massachusetts.

[6]The Superior Electric Company, Bristol, Connecticut.

The light was projected through the filters onto the cloth oviposition surfaces so it was necessary to use a condenser to assure equal distribution of the color over the cloth surface. The water-filled 250 ml. Florence flask between the light source and the filter was used to accomplish this and, at the same time, to keep the temperature from the light source well below 160°F. which was the maximum operating temperature for the filters.

Experimentation showed that a good distribution of light over the oviposition surfaces was obtained at 1.5 foot projection distance. This distance was enclosed by the black hoods to keep extraneous light from reaching the oviposition surface.

Since the projectors used for the competing wavelengths were both 1.5 feet away from the oviposition surface, the decrease in intensity below 1.6 foot-candles across the distance from

TABLE II

COMPARISON OF PERCENTAGES OF LIGHT TRANSMITTED TO THE VOLTAGE NECESSARY TO EQUALIZE INTENSITY AT 1.6 FOOT-CANDLES

WAVELENGTH		PERCENTAGE LIGHT TRANSMITTED	VOLTAGE
Yellow	580 mu	33	37V
Red	680 mu	31	40V
Blue	480 mu	15	55V
Green	530 mu	11	57V

projector to surfaces was the same for both surfaces. Since intensity of illumination of a surface is inversely proportional to the square of the distance from the light source, the approximate intensity 1.5 feet from the projector was 0.89 candles per square foot.

The light transmitted into the cage was further reduced considerably below 0.89 candles per square foot to the light that was transmittable through the cloth oviposition surfaces. These cloths diffused the light striking them, but since the light had to pass through thousands of random holes in the mesh of the cloth, it was very unlikely that cloth from the same bolt would reduce the intensities to any different extent on either side where different pieces of cloth were used. In order to test this, the same technique was used as that described below for determining the amount of polarized light that passed through the cloth into the cage.

As experiments were primarily tests on the oviposition response of the imago to the lighted surface, the cloth surface was essential to the work. In the experiment on polarized light, however, not only was the problem of intensity important, but also the problem of how much actual polarized light was getting through the cloth into the cage. To determine this, the

following method was used. A microscope lamp was turned up until a high light reading of 800 foot-candles was directed right against the photo electric cell in the light meter. Another reading was then taken with one of the neutral polaroid filters over the light source and an oviposition cloth over the filter. This reading dropped to 25 foot-candles. A second polaroid filter was then put over the cloth and orientated so that the lines of polarization of this filter were the same as the lines of polarization for the first filter. A third reading was then taken and the light dropped to 10 foot-candles The second polaroid filter was then rotated 90° blocking all so there remained but 14 percent polarized light. This figure, therefore represented the light which retained its single direction orientation passing through the thousands of holes in the cloth. All the rest of the light was again diffused and scattered by the cloth.

Different pieces of cloth used in the experiments were placed between the filters and readings taken. As no differences could be detected in the amount of polarized light getting through, it was apparent that the intensities of light going through any of the pieces of cloth would drop to approximately the same extent regardless of what piece was used on the cage.

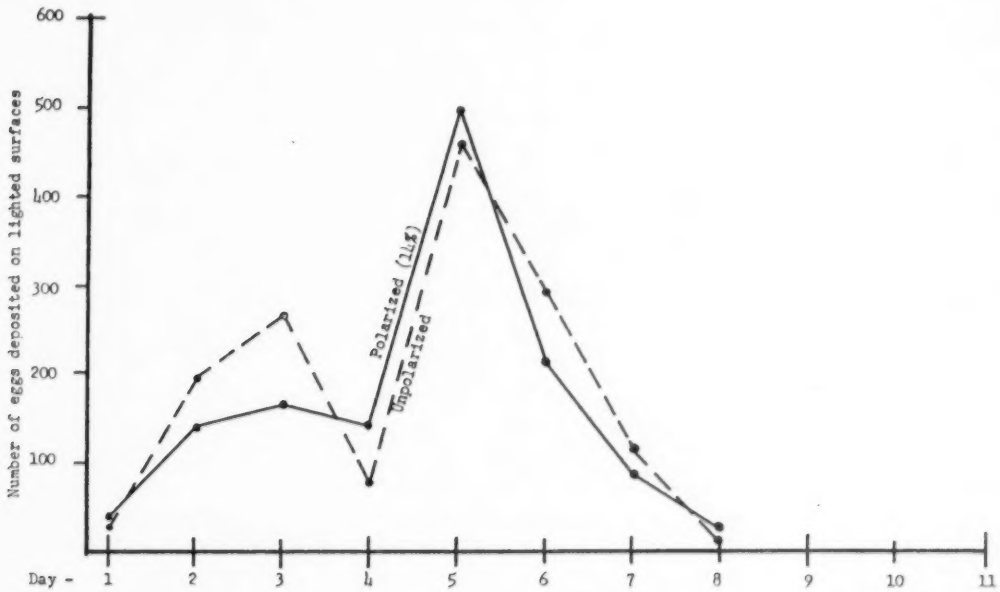

FIG. 2. Reaction of eight collected ovipositing female imagoes to partially polarized and unpolarized light of equal intensity as measured by eggs deposited on a suitable surface lighted with the two competing types of light, October 11 to 19, 1955.

polarized light coming through the cloth but allowing all unpolarized light to pass. The reading then dropped to 6.5 foot-candles. The percentage of polarized light was then easily calculated as follows: $\frac{10}{25}$ equaled the percentage of all light coming through both the filters and the cloth when the planes of polarization were the same; this was 40 percent of the original light: $\frac{6.5}{10}$ equaled the percentage of unpolarized light leaving the last filter when it was turned 90 degrees; this amounted to 65 percent of the light. Thirty-five percent of light thus remained polarized but this was only 35 percent of the original 40 percent that got through both filters

REACTION OF IMAGOES TO PARTIALLY POLARIZED AND UNPOLARIZED LIGHT

One of the neutral polarizers used in the experiments on color was placed in one of the projectors and the intensity of light adjusted to 1.6 foot-candles. This filter for all practical purposes polarized 100 percent of the light from the projector bulb. The cloth oviposition surface, however, cut the polarized light to 14 percent of the total. No filter was placed in the opposite projector and the direct unpolarized light from the incandescent lamp was projected on the oviposition surface. Eight moths collected from the black light trap were placed in the cage from October 11 to 18. The record of their oviposition response is shown in fig. 2 and

compared with the data of the rest of the color experiments in Table III. These data indicate that *Heliothis zea* showed no oviposition preference for a surface lighted with 14 percent polarized light above that of a surface lighted with unpolarized light. This experiment further served as a check on intensities by indicating that white lights of equal intensities were equally attractive to the imago.

REACTION TO VARIOUS WAVE LENGTHS OF LIGHT AS MEASURED BY EGGS DEPOSITED ON A LIGHTED SURFACE

Various wavelengths of light were projected on opposite cloth oviposition surfaces by means of the Polaroid variable color filters. The basic elements were several selective light polarizers that polarized part of the visible spectrum and transmitted the rest unpolarized. In this case, red, 680 mu; yellow, 580 mu; green, 530 mu; and blue, 480 mu and also a combination of red-blue, giving purple, and yellow-green were used.

Relative sensitivity of the imagoes to the various wavelengths was indicated by both actual observations of attracted imagoes and by the oviposition response of the imago, as calculated by the number of eggs deposited on the lighted oviposition surfaces. While using these actions of the imago to indicate such sensitivity on the part of the imago, one should not allow the relative sensitivity of one's own eyes to mislead one. As Bouma (1947) pointed out, it is known that the human eye is not equally sensitive to all spectral colors. Its sensitivity is high for colors in the middle of the spectrum, but gradually diminishes towards the extremities of the spectrum, red and violet. The results of experiments on relative luminosity curves of the human eye show that at low intensities where only the rods are active, the eyes' maximum sensitivity lies at 513 mu (blue-green) while at high intensities where only the cones play a part the eyes' maximum sensitivity lies at 555 mu (yellow-green). The cone curve extends much farther into the red end of the spectrum than does the low intensity rod curve (Weaver, 1937). These curves are based solely on the concept of apparent brightness of two differently colored lights.

These differences in sensitivity to colors by one's own eyes is easily demonstrated by the fact that although the intensities of opposite colors were equalized in this behavior cage, the moths could be observed much easier by the green and blue lights at complete saturation than by the red and yellow lights at complete saturation. This follows since at the low intensities of less than 0.89 foot-candles, the rods would be the most active.

In reviewing the literature, the only work found involving oviposition and color was that of Ilse (1928). He found that *Pieris brassicae*, a diurnal butterfly, showed a feeding choice for blue and

TABLE III

REACTION OF OVIPOSITING FEMALE IMAGOES TO VARIOUS WAVELENGTHS OF LIGHT AND TO 14 PERCENT POLARIZED AND UNPOLARIZED LIGHT OF EQUAL INTENSITIES AS MEASURED BY EGGS DEPOSITED ON A SUITABLE SURFACE LIGHTED WITH THE VARIOUS TYPES OF LIGHT, JULY 30–OCTOBER 19, 1955

Color	Days of Oviposition												Total No. Eggs per Color	Ratio to Nearest Tenth
	1	2	3	4	5	6	7	8	9	10	11	12		
Yellow vs. green	—	—	109	127	123	152	52	43	8	—	—	—	614	1 Y[c] to
	—	—	465	442	405	272	95	109	44	—	—	—	1832	3 G
Green vs. blue	—	—	100	142	190	136	50	40	73	—	—	—	731	1 G to
	—	—	240	280	205	166	125	85	418	—	—	—	1519	2.1 B
Red vs. green	—	—	0	11	36	112	37	31	16	26	87	0	356	1 R to
	—	—	10	79	300	513	140	112	117	245	91	29	1636	4.6 G
Total No. eggs by days[a]	—	—	924	1081	1259	1351	499	420	676	271	178	29	6688	
Red vs. yellow	109	329	95	93	221	231	394	327	130	71	0	22	2022	1 R to
	236	276	174	326	473	342	542	372	325	204	21	34	3685	1.8 Y
Yellow-green vs. purple	10	83	57	16	97	16	29	189	203	31	142	—	873	1 YG to
	21	205	312	94	226	374	382	370	102	82	326	—	2494	2.9 P
14% polarized vs. unpolarized	38	134	162	140	490	212	83	72	—	—	—	—	1281	1 Pol to
	32	190	264	75	455	292	112	18	—	—	—	—	1438	1.1 Unpol.
Total No. eggs by days[b]	446	1217	1064	744	1962	1467	1542	1658	760	388	489	56	11,793	

[a]Reared imagoes.
[b]Collected imagoes.
[c]Color.

purple papers and to a lesser extent for red and yellow; it disregarded green, blue-green, and grey altogether. However, the egg-laying female showed a "drumming" reaction of the forelegs to green and greenish blue papers, disregarding yellow and pure blue. Thus, the feeding response was at either end of the spectrum while the oviposition "drumming" response was in the middle of the spectrum. These colors were the reflected colors of the paper so the intensity of the reflected light probably varied.

Since green is approximately in the center of the spectrum and since at least the above lepidopteron was known to have an oviposition response to this color, it was chosen as a standard for the experiments. The results of the egg counts taken from the various competing lighted surfaces are given in Table III. These data show that more eggs were deposited on the surface lighted with green at the center of the spectrum than on the surfaces lighted with red and yellow at the

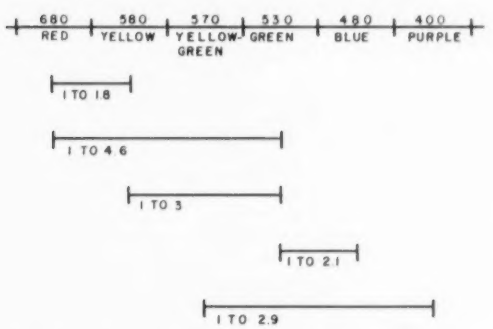

FIG. 3. Comparison of the ratio of eggs laid on the oviposition surfaces lighted with opposite competing wavelengths to the wavelengths in mu.

longer end of the spectrum, but that the surface lighted with blue, a shorter wavelength than green, received more eggs than did green. Since blue and green, which are close together at the shorter end of the spectrum, had been tested against each other, red and yellow, which are together at the longer end of the spectrum, were tested against each other. The yellow surface at the shorter end of the spectrum received more eggs than the red surface. Finally, since red and green, which are farther apart at the low to middle part of the spectrum, had been tested, yellow-green and purple, which are farther apart at the middle to high end of the spectrum, were tested against each other. The purple surface received more eggs than the yellow-green surface.

Figure 3 is a comparison of the ratio of eggs laid on the oviposition surfaces lighted with opposite competing wavelengths to the wavelengths in mu. The ratios were arrived at by dividing the total number of eggs on the surface receiving the most eggs by the total number of eggs on the surface receiving the least eggs.

Three main points are apparent from the above analysis. First, the response of *Heliothis zea* varies inversely with the wavelength. In other words, in any one test, the shorter wavelength receives greater response. In no case did a long wavelength receive more eggs than a shorter wavelength, except in two cases, each on a single night. Once when yellow was being tested against red, it dropped below red. This is explained by the fact that the light on the yellow side went out some time after 7:30 and was not seen until 12 midnight when work was resumed at the insectary. This accidental experiment indicates that when the imago is left with no alternative, a surface illuminated with red light is utilized rather than some other area of the cage. On another occasion when purple was being tested against yellow-green, the purple dropped below yellow-green. This may have been due to the low temperature drop on the night of October 8. For the 12-hour period from 6 p.m. to 6 a.m. the temperature averaged 44° with a low of 40°. This was the coldest night during the time of these experiments.

The second point noticeable in these data is that two wavelengths tested that are next to each other on the spectrum, *viz.*, red vs. yellow and green vs. blue, show less difference than do the wavelengths that are farther apart, *viz.*, red vs. green and yellow-green vs. purple.

The third noticeable point is that there is a much greater difference between the longer wavelengths and the middle, red to green, than there is from the middle to the shorter wavelengths, yellow-green to purple, but that where the wavelengths are close together, red vs. yellow and green vs. blue, there is only slightly less difference between the longer wavelengths, red vs. yellow, than shown between the short wavelengths, green vs. blue. It must be kept in mind that none of the wavelengths given in mu is exact but each is only approximate for each color at the most complete saturation of the color obtainable with the polaroid filters used.

In all these experiments (Table III), the colored oviposition surface with the least number of eggs did not show the steep peaks that the colored oviposition surface with the largest number of eggs did. It was also noticed that in most of these experiments, there were two or three oviposition peaks, usually one during the first five or six days, followed by a drop and then another peak toward the end of the ovipositon period. Some of the imagoes used in these experiments were collected from the black light trap and thus their age was unknown; also the temperature had dropped during September and October when these collected imagoes were used. The temperature was not so uniform for the experiments

with the collected imagoes as it was in those run with the reared imagoes earlier in the season.

When the total number of eggs deposited by the reared imagoes is compared with the total number deposited by the collected imagoes, only one main peak is noticed for both. The reproductive stages of the collected imagoes were unknown but the reared imagoes never oviposited before the third day and their main period of oviposition was from the third to the sixth day. The collected imagoes' peak of egg laying was from the sixth to the ninth day. This was probably attributable to the colder weather which increased the length of life but slowed the activities of the imagoes. It is probable that those peaks are a function of both the temperature and the time at which most of the imagoes copulated in the cage. Some of the collected imagoes had copulated before being placed in the cage as shown by the fact that they began oviposition on the first day.

REACTION TO VARIOUS WAVE LENGTHS OF LIGHT AS MEASURED BY NUMBERS OF IMAGOES ATTRACTED TO THE WAVE LENGTHS

The following data were obtained by counting the number of imagoes resting on various lighted oviposition surfaces. Counts were made at approximately 10-minute intervals or six times per hour from 8 p.m. until 5 a.m. except in the case of yellow vs green when the counts were stopped at 1 a.m. instead of at 5 a.m. A final single count was made at 9 a.m. when the observation hood was opened to let in daylight. This final count was usually one of the lowest as the moths had ceased activity by this time even though the hood was still down and the colored lights on. The counts represent the average for each hour on six different nights (Table IV).

On green there was peak activity that built up between 8 p.m. and 11 p.m. regardless of the color with which it competed; it then dropped off for the remainder of the evening. When the average for the high color went up, the average for the low color often went down, indicating that it was probably the same imagoes flying from one colored surface to the other. When green and blue competed, they started off about even, early in the night, but as time went on, the imagoes seemed to become more and more conditioned to blue and by early morning the attractiveness of blue had increased considerably over the green.

Figure 4 compares the ratio of numbers of

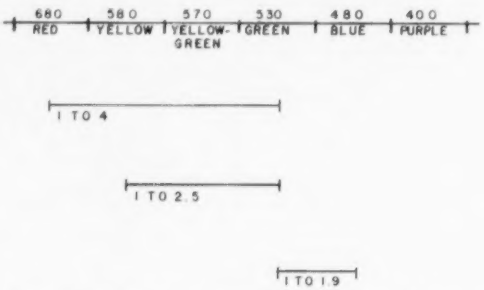

FIG. 4. Comparison of the ratio of the number of imagoes on surfaces lighted with the opposite competing wavelengths to the wavelengths in mu.

imagoes counted at the surfaces lighted with opposite competing wavelengths to the wavelengths in mu. The ratios were arrived at in the same manner as those in the section on oviposition.

This analysis verified two points of the results obtained in the section on oviposition: (1) response is always highest to the shortest wave-

TABLE IV

AVERAGE NUMBER OF IMAGOES ATTRACTED TO EACH COLOR AT SIX COUNTS PER HOUR ON SIX DIFFERENT NIGHTS

HOUR OF COUNT	RED VS. GREEN		YELLOW VS. GREEN		GREEN VS. BLUE	
8:00– 9:00 P.M.	2 2	11 4	3 3	3 5	6 2	7 5
9:00–10:00 P.M.	4 0	12 3	——	——	7 6	7 0
10:00–11:00 P.M.	2 1	7 8	2 3	12 5	6 1	8 2
11:00–12:00 P.M.	1 2	6 6	4 5	8 1	——	——
12:00– 1:00 P.M.	1 7	6 2	3 0	9 0	6 6	7 5
1:00– 2:00 P.M.	1 6	5 7	——	——	6 1	9 1
2:00– 3:00 A.M.	2 9	5 3	——	——	4 4	9 8
3:00– 4:00 A.M.	0 9	6 0	——	——	3 8	15 7
4:00– 5:00 A.M.	1 3	4 0	——	——	4 0	20 0
One count 9:00 A.M.	0	5 0	——	——	2 0	6 8
Total	17 9	70 3	13 1	33 1	46 8	91 6
Average of all hours on all nights	1 8	7 0	3 3	8 3	5 2	10 1
Comparison	1 to 4		1 to 2.5		1 to 1.9	

lengths; and (2) the closer together the wavelengths, the less the differences in response.

A comparison of the response measured by oviposition and that measured by counting the imagoes shows some striking similarities. The difference in the ratios between green vs. blue, in both experiments, is only 0.2 while the difference between yellow vs. green is 0.5. The difference between red vs. green in both experiments is 0.6 but both experiments show that the differences for this combination are far above the differences found for the other competing colors. The difference between red vs. green and the next highest color is 1.6 in the oviposition study, while the difference between red vs. green and the next highest color is 1.5 in the imago count study.

DISCUSSION

Not much is known about the intensities or wavelengths of light reflected from plants, especially during crepuscular periods when the imago is active. Seybold (Popp and Brown, 1936) showed that for green leaves, absorption increases as the wavelengths become shorter. This causes less of the short violet and ultra-violet wavelengths to be transmitted or reflected. Little ultraviolet is reflected from the surface of green foliage and maximum reflection is at 5400–5600°A., green-yellow (Weiss, 1943), a color to which the imago of *Heliothis zea* was certainly not especially attracted. As this is true, it becomes difficult to relate the color of the host plant to the wavelength preferences of the imago. On the other hand, it is apparent that the insects' activity might easily be related to the stimulus by the shorter wavelengths of light. When light passes through a medium of small particles such as our atmosphere, a part of the light is scattered by the particles in all directions, and the ratio of the intensities of the scattered and incident light varies inversely as the fourth power of the wavelengths (Duncan, 1946); thus, as the sun sinks, the light passes through a thicker and thicker layer of atmosphere, and since the light is being deprived of more and more of its short wavelengths in such tremendous amounts (up to the fourth power), the sun appears red, but the sky at right angles is becoming saturated with blue and violet as it receives the light that has been scattered by the particles of air. Therefore, the illumination of the total environment of the imago during crepuscular periods is made up of those short wavelengths to which the ovipositing insect is most sensitive. The insect is, no doubt, stimulated to activity by such light, but just what the actual effect is on the imago of this type of light reflected from green plants, one is unable to say. Another type of light is polarized light. Sky light is 70 percent polarized at right angles to the sun when the sun is high in the sky but there is very little polarized light at twilight, so any response of a crepuscular insect to polarized light would seem rather without utility.

Taking a cornfield as a whole, it could be possible that low intensity, short wavelengths of light reflected from the field would present some wavelength or pattern stimulus to imagoes and thus attract them for oviposition or feeding. Perhaps a contrast between the short wavelenghts of sky light and the longer reflected wavelengths from the plants present a stimulus to the imago.

It should be mentioned here that in regard to a black light trap, as many or more imagoes rested on the grass or in hedges nearby, as flew to the trap itself. It was particularly noticeable that the imagoes flew to this light in groups and with sudden spurts of activity. One could stand by the trap for minutes and never see an earworm moth, then suddenly there would be seven or eight. They were just as likely to come to the light reflected from a shirt as to the bulb itself. Quaintance and Brues (1905) mentioned the fact that the imagoes never came to an ordinary electric light but often congregated on stems of grass 20 to 50 feet from the light. This would certainly indicate attraction to low intensity light reflected from plant surfaces. Apparently, in the case of the black light trap, the imagoes were first attracted by the low intensity short wavelength light reflected from the surrounding plant surfaces, and then to the trap itself. The experiment, green vs. blue (Table IV), demonstrated that the imagoes, after a time, became conditioned to a short wavelength and that attraction to this wavelength increased with time. Conditioning might explain why the moths suddenly left the plants and flew to the trap itself where the wavelength emitted directly would be shorter than that reflected from green plants nearby.

SUMMARY AND CONCLUSIONS

The effect of preferred host plants and non-preferred plants as a stimulus to oviposition was studied. Results indicated that in cages with plants and also with a villous lighted oviposition surface the plants received considerably fewer eggs than did the villous oviposition surface.

A behavior cage was designed for the purpose of testing the response of the moths to various wavelengths of light projected on a villous oviposition surface. Polaroid variable-color filters were used to project the light on the surfaces and the intensities of light were equalized, using a light meter.

The following conclusions were reached from these experiments on light and color. (1) At equal intensities, the imagoes showed no difference in response to 14 percent polarized light and unpolarized light; (2) The higher response was always to the shorter wavelength; (3) The imago showed less response difference to competing wavelengths close together on the spectrum than to wavelengths farther apart; (4) The difference

in response to competing wavelengths close together at the long end of the spectrum was only slightly less than the difference in response to competing wavelengths close together at the short end of the spectrum; (5) The differences in response to competing wavelengths farther apart on the spectrum were greatest at the long end of the spectrum and less at the short end of the spectrum; (6) The response to green seemed to decline as the night progressed but the imagoes seemed to become conditioned to blue and the response to this color built up greatly as the night progressed; and (7) The various oviposition peaks were probably a function of temperature and time of copulation and not directly related to the light experiments.

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A STUDY OF THE HOST DISTRIBUTION AND SOME RELATIONSHIPS OF BITING LICE (MALLOPHAGA) PARASITIC ON BIRDS OF THE ORDER TINAMIFORMES[1]

PART II[2]

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CORRESPONDENCE BETWEEN SIZE OF HOST AND PARASITE

The effect of the environment upon the biota is often manifested by certain changes in the structure and size of the organism. In a genus of Mallophaga distributed over a group of birds, the size of the parasite is roughly related to that of the host (Harrison, 1915). Clay (1951) presents several instances of this correlation but the small number of her examples is insufficient to utilize statistical tests to check the validity of this idea.

The tinamous and their Mallophaga presented an opportune situation to investigate this phenomenon more inclusively. The wing length has been judged to be one of the best criteria to designate size in birds. An attempt was made to record the wing length of tinamous from the taxonomic literature. This proved unfeasible due to the various methods of measuring wings and also the tendency of some authors to cite just the range of the measurements. It was necessary to measure the 1500 tinamous in the Conover Collection of the Chicago Natural History Museum to have a set of reliable measurements. The wing of each individual was held flattened against a steel ruler and the length to the nearest millimeter was taken between the proximal end of the humerus and the apex of the longest primary. To arrive at a value which could be considered typical of the species or subspecies, a weighted mean was used which took into account differences in the number of males and females in the measured series.

The problem of picking structures to measure in the Mallophaga as indices of general size is more difficult. Abdomen and total length are some of the better criteria of size but are too variable within the small series of many species to be of use. The head length at the midline between the apex of the clypeal margin and the occipital margin usually proved to be one of the most constant within species yet showed consider-

[1]Portion of a dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the Department of Zoology, University of Chicago. This research was supported in part by a fellowship from the Department of Zoology, University of Chicago, and the Chicago Natural History Museum. The author wishes to extend his deep appreciation to Dr. Alfred E. Emerson for his valuable advice during these investigations.

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[2]Part I of this series appeared in the July, 1957, issue of these ANNALS (Volume 50, Number 4). Generic allocations of Mallophaga are those of Hopkins and Clay (1952), with the following exceptions: *Austrokelloggia* Carriker 1936 is not separable from *Kelloggia* Carriker 1903, *Heterogoniodes* Carriker 1936 is at most a well-defined species group of *Megapeostus* Carriker 1936, and *Heptapsus* Carriker 1936 is a synonym of *Pterocotes* Ewing 1929.

able range throughout the genus. The prothorax showed a more constant size but was usually the same length throughout a genus.

To ascertain if size of host and parasite show a mutual relationship, the correlation coefficient r was computed using the formula,

$$r = \frac{\Sigma xy - x\Sigma y}{\sqrt{(\Sigma x^2 - x\Sigma x)\quad(\Sigma y^2 - y\Sigma y)}}.$$

Student's *t*-test was calculated from

$$t = \frac{r\sqrt{N-2}}{\sqrt{1-r^2}},$$

to determine whether the observed correlation coefficients differed significantly from zero.

Due to the small sample size of less than 100, the standard error of r cannot be used to check its significance. However, Fisher's *z*-transformation may be used in establishing fiducial limits to the value of the correlation coefficient in the population from which the sample r has been drawn (Snedecor, 1946: 150).

Table I illustrates the method of computing r for the females from the genus *Strongylocotes*. The correlation coefficients, the *t*-test results and their probabilities (P) along with the 95% fiducial limits are recorded in Table II. These limits are those in which 95 cases out of 100 may be expected to contain the true population parameter. Genera such as *Megaginus* and *Pseudophilopterus* are not included as an inadequate number of specimens was available from different hosts. The small number of species in such genera as *Lamprocorpus*, *Trichodopeostus*, *Nothocotus* and *Cuclotocephalus* prevent a computation of r.

It may be noted from Table II that all of the

TABLE I

METHOD OF COMPUTING r FOR THE RELATION BETWEEN THE HEAD LENGTH OF FEMALE MALLOPHAGA OF THE GENUS *Strongylocotes* AND THEIR HOSTS

HOST	MALLOPHAGA	No.	BIRDS	No.
	Mean Head Length in mm. (x)		Mean Wing Length in mm. (y)	
Tinamus solitarius	1 071	2	262 8	4
T. major robustus	0 975	5	248 1	11
T. m. fuscipennis	0 975	2	243 4	15
T. m. peruvianus	0 954	3	240 3	22
T. osgoodi osgoodi	1 014	2	245 9	9
Nothocercus j. julius	0 972	5	197 3	8
N. bonapartei frantzii	0 888	6	224 2	5
Rhynchotus r. rufescens	0 976	13	203 1	27
R. r. maculicollis	1 020	9	214 1	10
Nothura boraquira	0 778	2	148 5	35
Crypturellus cinereus	0 643	3	172 1	30
C. soui meserythrus	0 822	2	133 7	25
C. s. modestus	0 683	4	133 9	22
C. s. harterti	0 763	2	131 0	29
C. s. nigriceps	0 739	2	129 2	8
C. s. inconspicuus	0 774	6	130 7	22
C. obsoletus obsoletus	0 792	3	165 9	20
C. o. punensis	0 744	2	161 6	9
C. o. griseiventris	0 782	2	165 9	7
C. brevirostris bartletti	0 743	3	140 6	13
C. undulatus undulatus	0 779	6	183 8	45
C. noctivagus garleppi	0 791	8	170 9	12
C. strigulosus	0 787	3	165 7	21
C. cinnamomeus goldmani	0 785	2	167 6	5
C. c. intermedius	0 771	2	165 5	10
C. c. vicinior	0 810	4	170 2	22
C. c. delattri	0 813	3	167 7	6
C. boucardi boucardi	0 782	9	172 4	22
C. barvirostris	0 645	2	117 1	43
C. tataupa tataupa	0 733	5	132 1	49

$\Sigma x = 24.804$ $\quad \Sigma y = 5305.3$

$N = 30$ $\quad N = 30$

$\Sigma x^2 = 20.890016$ $\quad \Sigma y^2 = 987595.15$

$\bar{x} = 0.8268$ $\quad \bar{y} = 176.843333$

$\Sigma xy = 4506.0099$

$$r = \frac{4506.0099 - 0.8268(5305.3)}{\sqrt{(20.890016 - 0.8268(24.804))\ (987595.15 - 176.843333(5305.3))}}$$

$r = +0.8706$

correlation coefficients are strongly positive, and as indicated by the *t*-test, differ significantly from zero. The reliability of *r* is fairly good with the exception of the *Heptapsogaster minor* group. In this instance, *r* tends not to be very reliable as a consequence of the small sample size.

It seems reasonable to state that the data indicate a well-defined relationship between size of host and size of parasite. A probable causal agent in this instance might be one of limitation of territory. Small species of tinamous as *Crypturellus soui* harbor approximately the same number of species of Mallophaga as much larger birds like *C. boucardi*. Apparently the same number of niches are available on both these host species although the size of the *Lebensraum* varies greatly. Consequently, there may have been a selection for size in these Mallophaga in their environment. Food supply probably does not play a role as there is an abundance regardless of host size.

From the viewpoint of the ecosystem, the most significant finding is that the entire Mallophaga fauna react as a whole to their environment. For instance, one may examine all twelve species from *Crypturellus soui* and note that almost every species is smaller than its counterpart on *C. boucardi*.

RELATION BETWEEN NUMBERS OF BIRDS INFESTED AND MALLOPHAGA SPECIES PRESENT

In studying the distribution of plant and animal species in communities and their subdivisions, the characteristic of "over-dispersion" or "contagious distribution" has been shown to be of general occurrence. This subject has been the topic of recent investigations (Fisher, Corbett, and Williams, 1943; Cole, 1946; and Bliss and Fisher, 1953). The main thesis of these papers seems to be concerned not as to the actual presence of over-dispersion but what type of mathematical model best fits the situation.

Communities of ectoparasites are among the most favorable types to analyze by this technique. The ease of collecting an entire population of obligatory ectoparasites such as Mallophaga, Anoplura, and Acarina from a single bird or mammal plus the concept that each individual in the host species population is a small ecological community creates ideal conditions for a study of this sort.

If every bird were equally liable to be infested with different numbers of species of Mallophaga, the differences between various individuals would be purely random and the distribution would conform to the Poisson series (Bliss, 1953). As Bliss points out, a Poisson distribution may be recognized by its expected variance being equivalent to the mean. In cases where the variance is significantly greater than the mean, "over-dispersion" is present. The negative binomial has been shown by Bliss to be as useful as any of the other distributions, such as Fisher's logarithmic series and the Neyman contagious type A, in studies on ectoparasites. This present study has utilized the Poisson, negative binomial, and logarithmic series distributions in an analysis of the Ischnoceran populations. The methods of fitting these distributions have been discussed in the papers of Fisher, Corbett, and Williams (1943) and Bliss and Fisher (1953). The estimate for the negative binomial has the exponent *k* computed by the method of maximum likelihood, which tends to give a more efficient fit than one based either upon the first and second moments or upon the ratio of the total number of units in the sample to the number of units without organisms. The observed distributions of

TABLE II

CORRELATION COEFFICIENTS BETWEEN SIZE OF HOST AND SIZE OF PARASITE

MALLOPHAGAN GENUS	STRUCTURE MEASURED	SEX	NO. (*N*) OF HOST AND PARASITE POPULATIONS	*r*	*t*	*P*	95% FIDUCIAL LIMITS	
							Lower	Upper
Pseudolipeurus	Head length[a]	♂♂	16	+ 8138	5 2396	< 001	+ 533	+ 933
" "	" "	♀♀	17	+ 8214	5 5777	< 001	+ 567	+ 934
Strongylocotes	Head length[b]	♂♂	23	+ 8388	7 0603	< 001	+ 628	+ 935
" "	" "	♀♀	30	+ 8706	9 3636	< 001	+ 744	+ 937
Kelloggia (s.l.), including *Austrokellogia*	Prothorax with	♂♂	47	+ 7482	7 5649	< 001	+ 586	+ 852
		♀♀	39	+ 8161	8 5899	< 001	+ 674	+ 902
Physconella	Head length[b]	♂♂	17	+ 8284	5 7278	< 001	+ 578	+ 936
" "	" "	♀♀	17	+ 8078	5 3076	< 001	+ 535	+ 928
Megapeostus	Head length[b]	♂♂	26	+ 9223	11 6910	< 001	+ 832	+ 965
" "	" "	♀♀	25	+ 8874	9 2249	< 001	+ 760	+ 950
Pectenosoma	Thorax length	♂♂	19	+ 8529	6 7357	< 001	+ 651	+ 942
" "	" "	♀♀	18	+ 8680	6 9921	< 001	+ 674	+ 950
Heptapsogaster minor group	Head length[b]	♂♂	8	+ 8163	3 4616	01	+ 263	+ 965
	" "	♀♀	9	+ 7425	2 9328	02	+ 155	+ 942

[a]Measured at midline between anterior edge of dorsal anterior plate and occipital margin.
[b]Measured at midline between anterior clypeal margin and occipital margin.

Mallophaga species per bird skin and the expected frequencies computed from the previous mentioned distributions are shown in Table III.

Table IV lists the Chi square (X^2) values, degrees of freedom (n) and probability (P) for each type of distribution fitting the observed frequencies. Although P is below the usual .05 level of significance for any one of the distributions for *Crypturellus* and *Tinamus*, the Chi square values for the negative binomial are the lowest of the three distributions. This lack of agreement may be attributed to the small value of n.

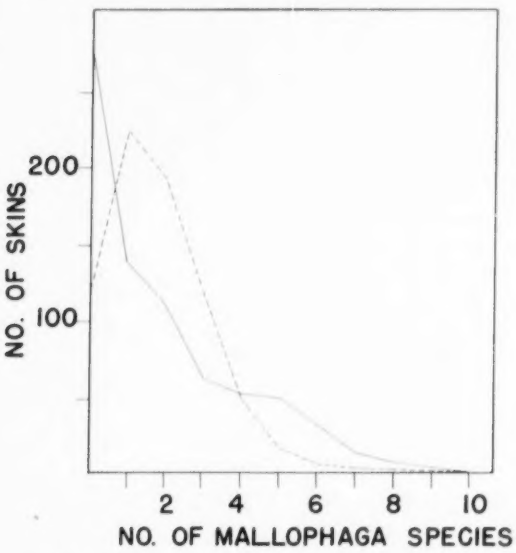

FIG. 1.—Graph showing observed and expected (Poisson) number of different species of Mallophaga encountered on skins of the host genus *Crypturellus*. The observed distribution is represented by a solid line while the calculated Poisson is indicated by a hyphenated line. As an example, three species of lice were found on 64 skins while if they had been randomly distributed (Poisson), three species would have occurred on 116 skins.

Bliss (1953) believes that better agreement can often be achieved by testing the agreement of the observed with the expected second and third moments of the negative binomial. *Nothocercus* shows a significant fit ($P = .40$) to the logarithmic series. The value of N (the number of skins observed) was fairly small in this instance in contrast to the much larger series of *Crypturellus* and *Tinamus*. It should be mentioned that when the zero class is disregarded, the negative binomial converges to the logarithmic series. The balance of the genera, particularly *Rhynchotus* and *Nothura*, show agreement with the negative binomial and even closer conformity to the Poisson series. These last four genera have a maximum of two to five species of Mallophaga occurring on a single skin while *Crypturellus*, *Tinamus* and *Nothocercus* may harbor up to eight or nine species simultaneously. Bliss (1953) states, "This phenomenon of substantial agreement with the Poisson at low densities and with the negative binomial at higher densities has been observed with both plant and animal populations".

A portion of the data from Table III has been graphed in figures 1 and 2. At the level of four species per skin for *Crypturellus* and three species per skin for *Tinamus*, there is a crossing of the curves for the observed and Poisson values. For the number of species above this point, a greater number are encountered on an individual host than could be expected by chance. An interspecific aggregation is present which appears to make the bird more favorable for multiple infestation once a minimal number of species are present. There is evidently a conditioning of the environment by the presence of several species with possible diversified feeding habits which allow additional species to occur.

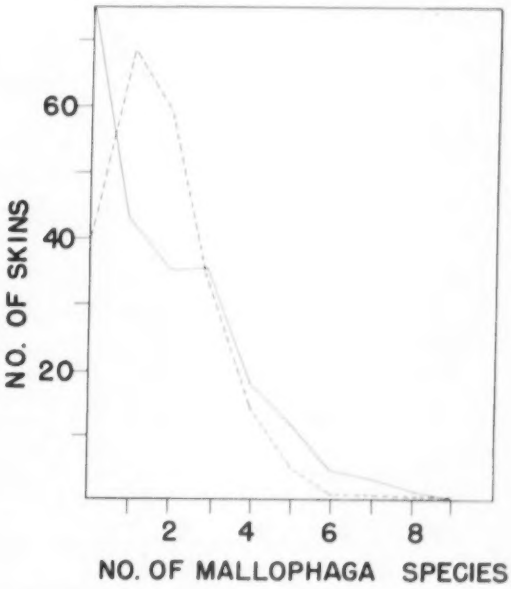

FIG. 2.—Graph showing observed and expected (Poisson) number of different species of Mallophaga encountered on skins of the host genus *Tinamus*. The observed distribution is represented by a solid line while the calculated Poisson is indicated by a hyphenated line.

ASSOCIATION OF MALLOPHAGA SPECIES ON HOSTS OF THE GENUS *Tinamus*

A paper by Cole (1949) provides a method of measuring the amount of interspecific association between pairs of species. By use of his coefficient, it is possible to express the positive or negative association of two species beyond that which

TABLE III

OBSERVED AND CALCULATED NUMBERS OF SPECIES OF LICE PER SKIN

No. of Species of Mallophaga per Skin (x)	No. of Bird Skins Observed (f)	Expected Number of Skins		
		Negative Binomial	Logarithmic Series	Poisson
	Genus *Crypturellus*			
0	275	260 04	———	124 48
1	140	171 47	212 00	221 02
2	113	110 43	88 78	196 21
3	64	70 55	49 57	116 13
4	53	44 89	31 14	51 55
5	50	28 50	20 86	18 30
6	12	18 06	14 56	5 42
7	15	11 43	10 45	1 37
8	9	7 23	7 66	0 30
9	4	4 57	5 70	0 06
10+	0	7 83	19 28	0 16
	735 = N			
	Genus *Tinamus*			
0	75	66 83	———	39 61
1	43	58 65	72 08	68 61
2	35	40 20	29 34	59 42
3	36	24 99	15 93	34 31
4	18	14 73	9 73	14 86
5	12	8 40	6 33	5 15
6	4	4 68	4 30	1 49
7	3	2 57	3 00	0 37
8	1	1 39	2 14	0 07
9+	0	1 56	6 15	0 11
	224 = N			
	Genus *Nothocercus*			
0	4	7 65	———	3 43
1	19	10 45	20 89	9 19
2	8	9 69	8 82	12 31
3	4	7 68	4 96	11 00
4	5	5 45	3 14	7 37
5	2	3 62	2 12	3 95
6	2	2 31	1 49	1 76
7	3	1 42	1 08	0 68
8	3	0 85	0 80	0 23
9+	0	0 88	2 70	0 08
	50 = N			
	Genus *Rhynchotus*			
0	10	7 34		7 17
1	7	14 19		14 21
2	17	13 89		14 07
3	11	9 17		9 26
4	6	4 60		4 60
5	1	1 87		1 82
6+	0	0 94		0 87
	52 = N			

TABLE III (*Continued*)

No. of Species of Mallophaga per Skin (x)	No. of Bird Skins Observed (f)	Expected Number of Skins		
		Negative Binomial	Logarithmic Series	Poisson
Genus *Nothoprocta*				
0	66	61.87		61.10
1	43	58.14		58.81
2	42	28.01		28.30
3	9	9.21		9.08
4+	0	2.77		2.71
	160 = N			
Genus *Nothura*				
0	144	144.53		144.54
1	64	60.05		60.06
2	8	12.48		12.48
3	1	1.73		1.73
4	2	0.18		0.18
5+	0	0.03		0.01
	219 = N			
Genus *Eudromia*				
0	20	20.73		20.72
1	14	14.15		14.15
2	7	4.83		5.07
3+	0	1.29		1.06
	41 = N			

would occur if the species were randomly distributed. Cole's coefficient has the advantage of covering the range of +1 to −1, with the former indicating perfect association, the latter negative association and zero signifying random association. Species of Mallophaga occurring on the genus *Tinamus* were utilized for this special study. Each host specimen was considered as a single sample. The three species groups of *Heptapsogaster* (*minuta*, *grandis* and *parvula*) were not used as the nymphal stages of each could not be distinguished with sufficient certainty under the dissecting microscope. For the balance of the species, their presence could be determined accurately just by the presence of nymphs.

For computing Cole's coefficient, the data were set up in 2 X 2 tables as follows, with species A being the "least frequent of the two species under consideration."

		Species B		
		present	absent	
Species A	No. of times present	a	b	$a+b$
	No. of times absent	c	d	$c+d$
		$a+c$	$b+d$	$a+b+c+d=n$

The coefficient of association, with its standard error; when $ad \gtrless bc$, is,

$$C \pm \sigma_C = \frac{ad-bc}{(a+b)\ (b+d)} \pm \sqrt{\frac{(a+c)\ (c+d)}{n(a+b)\ (b+d)}}.$$

When $ad < bc$, two other formulae cited by Cole (1949) are used.

The results are listed in Table V. With the exception of the coefficient of association between *Pseudolipeurus* and *Rhopaloceras*, all combinations of species achieve a positive association between 16% and 70% of the possible time.

The Ischnoceran fauna of a bird may be divided into a number of morphological types which occupy different ecological niches on the same bird (Clay, 1950). On the head and neck is found a round-bodied type with a large head to accomodate the enlarged mandibles and musculature. The wing niche is occupied by an elongate type with a narrow head and much smaller mandibles. Other morphological types are intermediate between these two and are presumed to inhabit the back and other niches. Of the Mallophaga occurring on *Tinamus*, *Pseudolipeurus* is found on the wings, *Rhopaloceras* on the head and the others such as *Pterocotes*, *Strongylocotes*, *Ornicholax* and *Kelloggia* on the dorsum. The coefficients of association showed the concurrence of several species on the same

TABLE IV

CHI SQUARE VALUES FOR EACH TYPE OF DISTRIBUTION AND THEIR PROBABILITIES

HOST GENUS	POISSON			NEGATIVE BINOMIAL			LOGARITHMIC SERIES		
	X^2	n	P	X^2	n	P	X^2	n	P
Crypturellus	466.0260	5	.0005	28.3387	7	.0005	113.7655	8	.0005
Tinamus	74.7845	4	.0005	13.4414	4	.005	57.3921	4	.0005
Nothocercus	16.8886	3	.0005	11.7644	3	.005	1.6218	2	.40
Rhynchotus	5.7118	3	.10	5.7700	2	.05			
Nothura	1.0633	1	.20	2.4491	1	.10			
Nothoprocta	11.9356	2	.001	14.0236	2	.0005			
Eudromia	0.1501	1	.60	0.1681	0	———			

host is a normal situation and is to be expected with reasonable certainty in this group of ectoparasites. This persistence of an interspecies population may be interpreted as signifying a lack of competition between the Mallophaga on the back and also the possible cooperative interaction previously mentioned. This lack of competition is attributed to several density-dependent factors inherent to this particular host-parasite relationship. The preening activity of the host is an important method of regulating population size of the lice. Populations of lice increase tremendously in instances where a bird's bill is deformed to the point where it cannot preen itself (Worth, 1940, and Kartman, 1949). The common occurrence of taking dust baths in certain groups of birds, including the tinamous, is considered by some workers to be of significance in affecting population size. A final factor, possibly the most important, is the diversity of niches which permits a relatively large number of species to coexist in a rather limited microgeographic area. Chandler (1916) has pointed out that the tinamous are the only group of birds with plumules in the feather tracts themselves but not in the intervening apteria. This lack of plumules between the separate feather tracts may thus produce a greater diversity of habitat for Mallophaga than is found in other groups of birds.

TABLE V

COEFFICIENT OF ASSOCIATION BETWEEN MEMBERS OF SOME OF THE GENERA OF MALLOPHAGA PARASITIZING *Tinamus*

PAIRS OF MALLOPHAGA	$C \pm \sigma$
Kelloggia and *Pterocotes*	+0.473 ± .112
Kelloggia and *Strongylocotes*	+0.696 ± .118
Kelloggia and *Ornicholax*	+0.545 ± .125
Kelloggia and *Pseudolipeurus*	+0.343 ± .175
Pterocotes and *Strongylocotes*	+0.261 ± .187
Pterocotes and *Ornicholax*	+0.288 ± .125
Pterocotes and *Pseudolipeurus*	+0.290 ± .104
Strongylocotes and *Ornicholax*	+0.305 ± .067
Strongylocotes and *Pseudolipeurus*	+0.307 ± .099
Ornicholax and *Pseudolipeurus*	+0.158 ± .100
Rhopaloceras and *Kelloggia*	+0.171 ± .187
Rhopaloceras and *Pterocotes*	+0.370 ± .104
Rhopaloceras and *Strongylocotes*	+0.328 ± .106
Rhopaloceras and *Ornicholax*	+0.328 ± .107
Rhopaloceras and *Pseudolipeurus*	+0.016 ± .072

The possible effect of diversity of the habitat has been shown to be important in the distribution of certain fleas (Evans and Freeman, 1950). In studying the association of *Ctenophthalamus agyrtes nobilis* (Rothschild) and *Malaraeus penicilliger* (Grube) on *Apodemus s. sylvaticus* (Linné) and *Clethrionomys glareolus brittanicus* (Miller), they found Cole's coefficient of interspecific association to be $-0.808 \pm .175$ for the former host and $+0.537 \pm .109$ for the latter one. They attribute this difference of interacting behavior to the fur characteristics of *Clethrionomys*—somewhat longer and coarser than that of *Apodemus*. Evans and Freeman conclude that this may allow *C. agyrtes* and *M. penicilliger* to exist side by side on that host in contrast to the direct competition which may exist on *Apodemus*.

SUMMARY

1. A well-defined relationship exists between the size of host and parasite. This was demonstrated by use of the product-moment correlation coefficient, r, which was computed for seven Mallophaga genera and their hosts. Small host species harbor approximately the same number of parasite species as large-sized hosts but possess a fauna containing much smaller species.

2. A study of the relation between the numbers of birds infested and the number of different species of Mallophaga present has indicated that a greater number of species occur on a given host than would be expected by chance. An interspecific association is present which is favorable for the occurrence of mixed species populations.

3. A positive association between pairs of Mallophaga species on the genus *Tinamus* was demonstrated by use of Cole's coefficient of association. This positive association has been in part attributed to a possible cooperative interaction between species and a diversity of the habitat which permits several species to coexist in a limited microgeographic area.

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DIFFERENTIATION OF SECOND AND THIRD STAGE LARVAE OF CALIFORNIA CULEX (DIPTERA: CULICIDAE)[1]

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Species identification on the basis of the fully grown larva has reached a state of perfection in mosquitoes hardly equalled by any other group of insects of comparable size. However, the substantial field of literature on larval taxonomy has included little on the earlier larval stages even though these are frequently collected in the field. It is not uncommon to find a mixture of larvae of all stages in a single pool. As climate has a variable influence on oviposition and eclosion in different species, such a mixture may contain fourth stage larvae of one species, third and second stages of another, and second and first stages of two more. Routine practice usually results in identification of the oldest larvae only.

In a previous paper (Bohart, 1954), California species of *Aedes* have been compared in the first larval stage. Unfortunately, first stage *Culex* do not appear to have enough constant characters to permit easy differentiation. On the other hand, the second and third stages are reasonably distinctive. As these have not been described previously for most of the 12 California species, we have attempted a key and a short diagnosis of each stage. Obviously, the observed limits of hair branching, number of comb scales, and the like is conditioned by the material available for study, so this has been indicated in each case.

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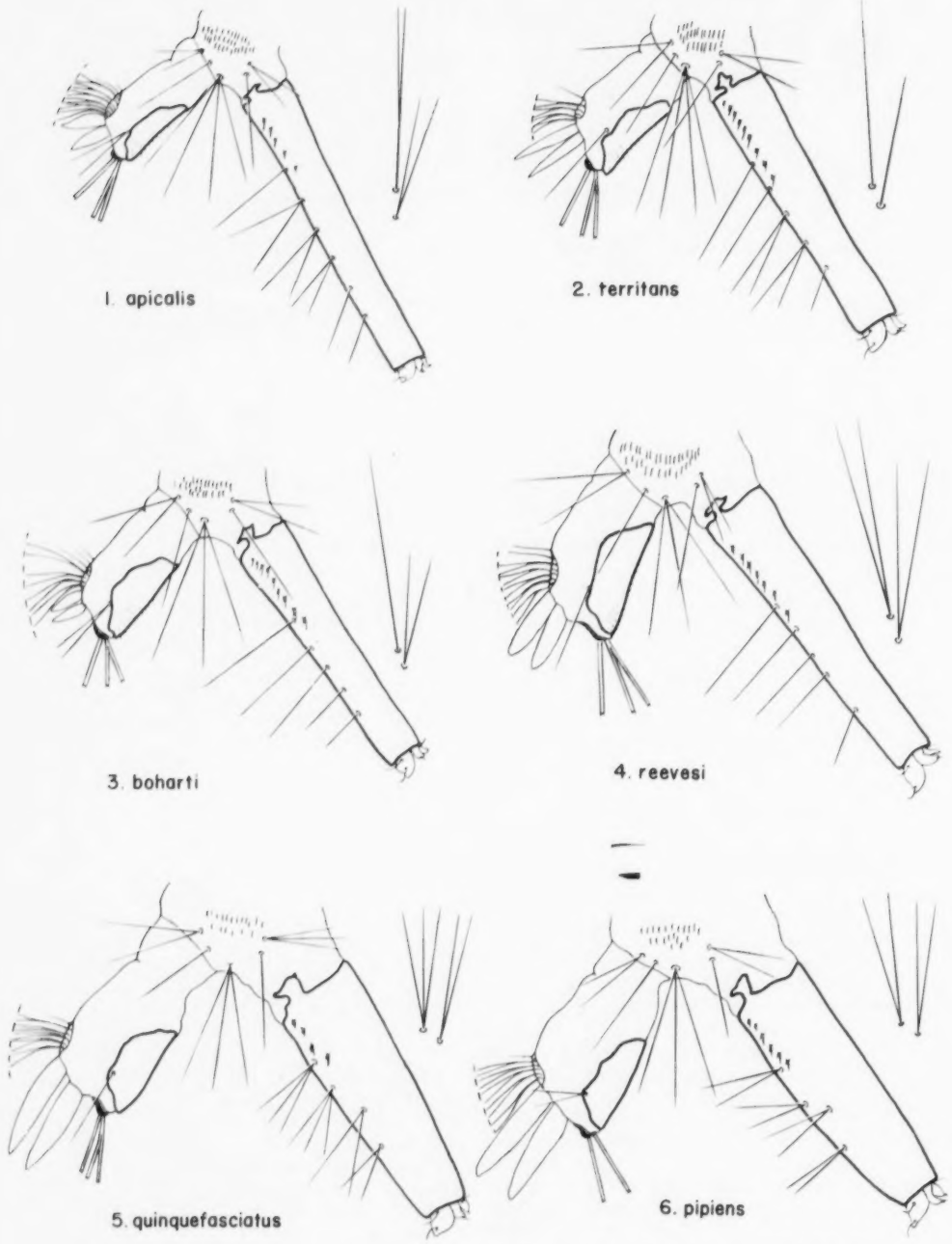
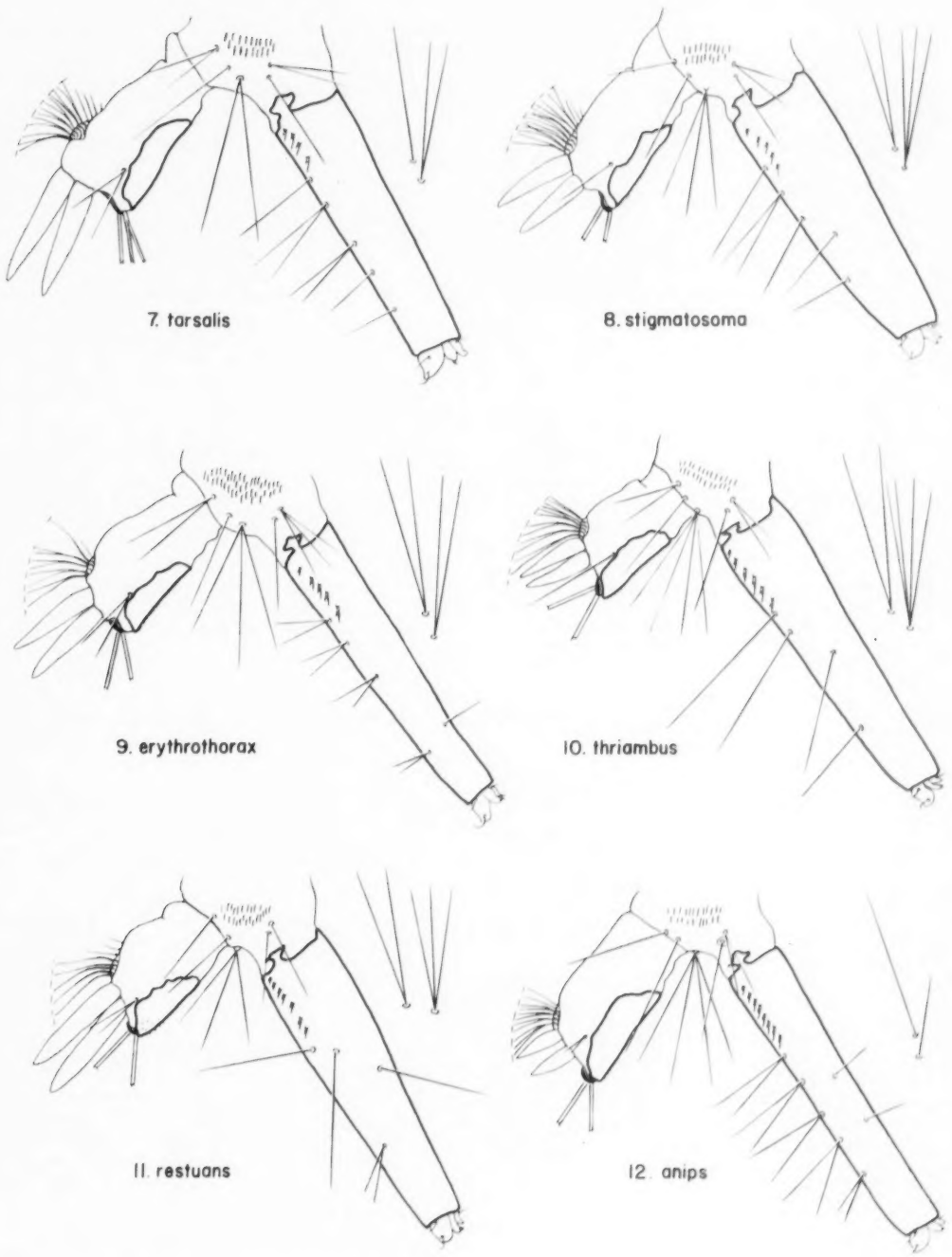
In general the same structures used in the fourth stage are of value in the second and third even though they may be less developed. There is an obvious tendency for hairs to become more branched at each molt. For instance, a hair may be single in the first stage, double in the second, triple in the third, and many-branched in the fourth. Similarly the sclerotization of the siphon and anal segment increase progressively. In all of the Californian species the fully grown larva has the anal ring or saddle complete. In the earlier stages the position of the lateral hair of the anal segment relative to the saddle has taxonomic significance. The number of comb scales becomes greater with age, and the average differs between species. For example, in our material the average numbers of scales in the comb patch of the first to fourth stages of *Culex stigmatosoma* are 9, 17, 29, and 36. In *erythrothorax* the comparable figures are 12, 38, 67, and 81. Another feature of interest is the degree of branching of the inner caudal seta of the anal segment. This is single in both second and third stages of *restuans;* usually single in the second and double or triple in the third in *erythrothorax, stigmatosoma, thriambus,* and *pipiens;* and often or usually double in the second and multiple in the third in the rest of the species. A possible indication of phylogenetic significance is the presence in the subgenera *Neoculex* and *Melano-*



FIGS. 1–6, second stage larvae of *Culex*, terminal segments and head hairs on left side of body.



FIGS. 7–12, second stage larvae of *Culex*, terminal segments and head hairs on left side of body.

conion of stout, black clypeal spines instead of the usually pale, attenuate ones in the typical subgenus *Culex*.

KEY TO SECOND AND THIRD STAGE LARVAE OF CALIFORNIA *CULEX*

1. Clypeal spine stout to tip; usually black throughout 2
   Clypeal spine attenuate toward apex, often pale 6
2. Siphon with two pairs of subdorsal hairs, inner caudal seta single, second pentad hair inserted on a sclerotized plate ..... **anips**
   Siphon without subdorsal hairs, inner caudal seta rarely unbranched; second pentad hair not inserted on a plate 3
3. Siphon, excluding acus and valves, at least four times as long as saddle of anal segment; pigmentation of abdominal segment IV about equal to that of III and V (best seen in living or freshly killed specimens) ..... **apicalis**
   Siphon, excluding acus and valves, less than four times as long as saddle of anal segment 4
4. Upper and lower head hairs (5 and 6) single; pigmentation of abdominal segment IV about equal to that of III and V ..... **territans**
   Upper head hair (5) double; pigmentation of abdominal segment IV light as compared with that of III and V 5
5. Lower head hair (6) single ..... **boharti**
   Lower head hair (6) double ..... **reevesi**
6. Not more than four pairs of siphon hairs, basal three long, strong, out of line, and almost always single; inner caudal seta single, at least in second stage 7
   With five to six pairs of siphon hairs or with three basal ones not long, strong and single 8
7. Antennal tuft inserted near middle of antenna, mental plate teeth each three or more times as high as wide ..... **restuans**
   Antennal tuft inserted near distal two-thirds of antenna, mental plate teeth less than three times as high as wide ..... **thriambus**
8. Lateral hair of anal segment plainly inserted on saddle; siphon with four pairs of usually multiple tufts which are not in line ..... **pipiens** and **quinquefasciatus**
   Lateral hair of anal segment inserted tangent to or near saddle 9
9. Siphon without sublateral hairs ..... **tarsalis**
   Siphon with one or two hairs out of line sublaterally 10
10. Comb of fewer than 35 scales (usually fewer than 20 in the second stage and fewer than 30 in the third) ..... **stigmatosoma**
    Comb of more than 35 scales (more than 35 in the second stage and usually more than 50 in the third) ..... **erythrothorax**

Notes on variation in chaetotaxy as well as the source and number of specimens examined are given below. Head hairs 5 and 6 are designated upper and lower head hairs respectively. The five lateral hair tufts in a semi-circle below the comb patch are called the pentad hairs and the branches of each from dorsal to ventral are indicated in the pentad formula. The inner caudal seta is abbreviated to ics.

Culex (Melanoconion) anips Dyar

(Fig. 12)

Instar II: Head hairs single, 19–22 comb scales, pentad formula 1–1–4–1–2, siphonal tufts mostly double but sometimes single or triple, ics single.

Material: 2 in second stage, near Descanso, Baja California, Mexico.

Culex (Neoculex) apicalis Adams

(Fig. 1)

Instar II: Upper and lower head hairs usually double but lower are commonly single from middle to base, 27–36 comb scales (usually 32–33), pentad formula usually 2–1–4–1–2, siphonal tufts single or double, ics single or occasionally double.

Instar III: Upper and lower head hairs double, lower are usually single at base, 44–76 comb scales (usually 54–64), pentad formula from 2–1–2–1–2 to 4–1–8–1–3, siphonal tufts occasionally single but usually double or triple, ics double or rarely triple.

Material: 32 in second stage and 27 in third stage from Green Valley, Solano Co., Calif.; Ojai, Ventura Co., Calif.; Gaviota Pass, Santa Barbara Co., Calif., Oak Creek Caynon, Coconino Co., Arizona (type locality).

Culex (Neoculex) boharti Brookman and Reeves

(Fig. 3)

Instar II: Upper head hairs double, lower head hairs single, 20–35 comb scales (usually 26–35), pentad formula usually 2–1–3–1–2 but varying to 3–1–4–1–2, siphonal tufts single or rarely double, ics double.

Instar III: Upper head hairs double or rarely single, lower head hairs single, 40–62 comb scales, pentad formula 2–1–3–1–2 to 3–1–6–1–3, siphonal tufts mostly double but sometimes single or triple, ics double or sometimes triple.

Material: 39 in second stage and 28 in third stage from Trinity, Marin, Napa, Solano, Santa Barbara, and Ventura Counties, California.

Culex (Neoculex) reevesi Wirth

(Fig. 4)

Instar II: Head hairs double, 24–47 comb scales (usually 27–38), pentad formula usually 2–1–3–1–2 but varying from 1–1–2–1–1 to 3–1–3–1–3, siphonal tufts single or sometimes double, ics usually double but rarely single or triple.

Instar III: Head hairs double, upper ones rarely triple, 49–73 comb scales, pentad formula 2–1–4–1–2 to 4–1–7–1–3, siphonal tufts usually double but sometimes single or triple, distal tuft often single, ics double or triple.

Material: 26 in second stage and 20 in third stage from Black Lake, San Luis Obispo Co., Calif.

Culex (Neoculex) territans Walker

(Fig. 2)

Instar II: Head hairs single, 21–29 comb scales, pentad formula 2–1–3–1–1 to 2–1–4–1–2,

siphonal tufts single or double, ics single or double.

Instar III: Head hairs single, 44–55 comb scales, pentad formula 2–1–4–1–2 to 3–1–6–1–3, siphonal tufts double or triple, ics double.

Material: 6 second stage and 5 third stage larvae from Weaverville, Trinity Co., Calif.; and Canyon Dam, Plumas Co., Calif.

Culex (Culex) erythrothorax Dyar
(Fig. 9)

Instar II: Head hairs double, 36–43 comb scales, pentad formula 2–1–2–1–2 to 3–1–4–1–3, siphonal tufts single or double, ics single.

Instar III: Upper head hair triple to quintuple but usually triple, lower head hair usually double but sometimes triple, 48–91 comb scales (usually 57–73), pentad formula 2–1–3–1–3 to 5–1–6–1–4, siphonal tufts usually double but sometimes single or triple, ics usually double but sometimes single or triple.

Material: 11 in second stage and 30 in third stage from Merced, Ventura, and Orange Counties, Calif.; and Descanso, Baja California, Mexico.

Culex (Culex) pipiens Linnaeus
(Fig. 6)

Instar II: Head hairs double or sometimes triple, 16–26 comb scales, pentad formula 2–1–3–1–2 or more rarely 1–1–3–1–1, siphonal tufts double or sometimes triple, ics single or rarely double.

Instar III: Head hairs triple or quadruple, rarely more, 36–52 comb scales, pentad formula 2–1–4–1–2 to 4–1–6–1–4, siphonal tufts mostly double but sometimes single or triple, ics single or double.

Material: 13 in second stage and 13 in third stage from Davis, Yolo Co., Calif.

Culex (Culex) quinquefasciatus Say
(Fig. 5)

Instar II: Head hairs double or triple, rarely quadruple, 16–23 comb scales, pentad formula usually 2–1–3–1–2 but varying to 2–1–4–1–3, siphonal tufts double or triple, rarely single, ics single or double.

Instar III: Head hairs triple or quadruple, rarely quintuple, 31–46 comb scales, pentad formula 3–1–4–1–3 to 4–1–6–1–4, siphonal tufts double to sextuple, ics double or rarely single.

Material: 27 in second stage and 27 in third stage from Manteca, San Joaquin Co., Calif.; and Springville and Visalia, Tulare Co., Calif.

Culex (Culex) restuans Theobald
(Fig. 11)

Instar II: Head hairs double or triple, 20–27 comb scales, pentad formula 1–1–3–1–1 to 2–1–3–1–2, siphonal tufts single except distal one which is sometimes double, ics single.

Instar III: Head hairs triple to quadruple, rarely quintuple, 43–49 comb scales, pentad formula 2–1–5–1–2 to 3–1–6–1–3, siphonal tufts usually single except for distal one which is often double and may be triple, ics single.

Material: 11 in second stage and 5 in third stage from Ojai, Ventura Co., Calif.; Peters Canyon, Orange Co., Calif.; and Descanso, Baja California, Mexico.

Culex (Culex) stigmatosoma Dyar
(Fig. 8)

Instar II: Head hairs double or triple, 14–22 comb scales, pentad formula 1–1–2–1–1 to 3–1–4–1–3, siphonal tufts single or double, rarely triple, ics usually single, rarely double.

Instar III: Upper head hair triple to quintuple, lower head hair double to quadruple, 22–40 comb scales, pentad formula 3–1–5–1–2 to 5–1–7–1–3, siphonal tufts single to sextuple, ics double or triple.

Material: 21 second stage and 76 third stage from Yolo and Solano Counties, Calif.

Culex (Culex) tarsalis Coquillett
(Fig. 7)

Instar II: Head hairs single to triple, upper head hair most often double, lower head hair usually single, 12–22 comb scales, pentad formula 1–1–2–1–1 to 3–1–4–1–2, siphonal tufts single or double, ics usually double, sometimes single.

Instar III: Upper head hair double to quadruple, lower head hair double or triple, 21–40 comb scales, pentad formula 3–1–4–1–2 to 4–1–6–1–3, siphonal tufts double to quadruple, rarely quintuple, ics double or triple, rarely quadruple.

Material: 35 in second stage and 41 in third stage from Butte, Napa, Yolo, Solano, and Kern Counties, Calif.

Culex (Culex) thriambus Dyar
(Fig. 10)

Instar II: Upper head hair triple to quintuple, lower head hair double or triple, 21–33 comb scales, pentad formula 2–1–3–1–2 to 4–1–5–1–3, siphonal tufts single, rarely double, ics single.

Instar III: Upper head hair quadruple to sextuple, lower head hair triple to quadruple, 43–55 comb scales, pentad formula 3–1–5–1–2 to 5–1–7–1–3, siphonal tufts single except distal one which is sometimes double, ics double, rarely single or triple.

Material: 25 in second stage and 20 in third stage from Ojai, Ventura Co., Calif.; Snelling, Merced Co., Calif.; and Descanso, Baja California, Mexico.

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THE DEVELOPMENT OF THE SALIVARY GLANDS IN ANOPHELES ALBIMANUS WIEDEMANN (DIPTERA, CULICIDAE)[1]

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A great amount of detailed information exists on the development of various organs in immature insects and on the differentiation of imaginal discs especially among the Diptera (Bodenstein, 1953). Except for a paper by Thompson (1905), it is altogether surprising to find that for mosquitoes there is apparently no description of the growth of the larval salivary glands or of the origin and development of the imaginal glands. Even the anatomy of the larval glands has received scant attention (Imms, 1907, Salem, 1931, Frizzi, 1947, Schildmacher, 1950), and this mostly in connection with other problems.

The present paper describes the anatomy of the pre-imaginal glands of *Anopheles albimanus* and gives detailed information on how the larval and adult salivary glands develop.[4] Brief anatomical comparisons are made between the larval glands of *Anopheles*, *Culex*, and *Aedes*.

MATERIALS AND METHODS

The mosquitoes used in this study were reared in an insectary held at 22±2°C, with a relative humidity ranging from 50% to 70%. The larvae were fed daily on dogfood and yeast. Adults were given 5% sugar solution and blood.

Since the duration of the various stages varied considerably, all studies were made on individually reared specimens of known history and precise chronological ages.

Salivary glands were examined in living intact larvae, in freshly dissected whole mounts from each stage in 0.85% NaCl (Jensen, 1955), either without staining or after staining with acetocarmine, or with Berger's modification (1938) of the Feulgen reaction. Material from each stage was fixed in Carnoy, Bouin, or formalin, then sectioned at 6 to 8 microns, and stained with Delafield's or Heidenhain's hematoxylin.

Measurements on whole glands and associated structures were made at magnifications of 210 to 430, and nuclei were measured at 980.

RESULTS

1. *Morphology of the larval glands.*—The salivary glands of *Anopheles albimanus* are paired organs which lie in the thorax on either side of the alimentary canal; they extend as far as the metathorax, where in most species portions of them are clearly visible directly through the cuticle. Each gland has two well-defined parts: a large terminal sac or distal portion (fig. 1, TS), and a smaller, spherical or globular anterior or proximal part (AS). The two portions are connected by a short neck or isthmus. When the glands are dissected out in 0.85% NaCl the anterior sac retains its spherical form, but the terminal part tends to collapse into an irregular shape as shown in figure 2. The glands are ensheathed by a fine basement membrane.

The terminal portion is composed of 50 to 60 cells which have large, round, centrally located nuclei, prominent nucleoli, and well-defined chromosomes (fig. 4). The anterior portion is made up of 12 to 15 cells which are much larger than those in the distal part, and its huge, round, central nuclei have giant, banded chromosomes (fig. 3). In *A. quadrimaculatus* the banding is visible in live whole mounted larvae. In general, the cells of both portions are roughly polygonal in

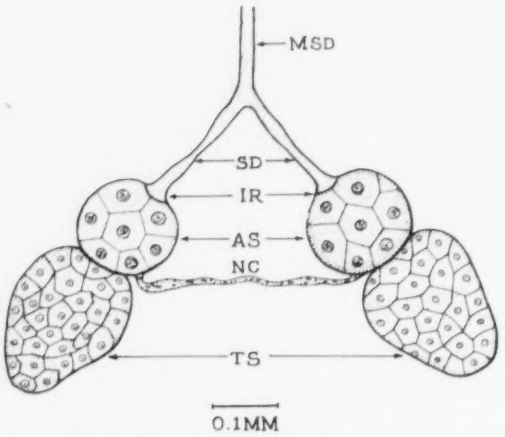

FIG. 1. The larval salivary glands of *Anopheles albimanus* showing the median salivary duct (MSD), the side ducts (SD), the anterior sac (AS), the ventral nephrocyte chain (NC), and the terminal sac (TS). The ring of tissue from which the adult glands differentiate is indicated at IR. The drawing is semi-diagrammatic.

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[4]Based on the Senior Author's Master's Thesis (1953), on deposit in the George Washington University Library.

shape. Cells in the proximal part of the gland are thick and bulge inwards, making the lumen small; at times cells in the distal part may also bulge slightly, but usually they are thin and flattened, leaving a large lumen. A compact band of very minute cells (fig. 1, IR, and fig. 5) encircles the anteriormost part of the gland where it empties into the salivary duct (fig. 1, SD). A slender syncytial chain of tissue extends between the two salivary glands, the ends being attached near the junction of the proximal and distal portions as shown in figure 1 (NC). This strand, when seen in freshly dissected material, contains many relatively large, pale greenish inclusions, and has seven or eight round nuclei in each portion of the chain. When larvae are fed ammonia carmine this tissue becomes filled with bright red granules like the pericardial cells. These cells were termed ventral nephrocytes by Metalnikov (1902), who first discovered them in *Culex*.

An examination of the salivary glands of *Anopheles quadrimaculatus, freeborni, aztecus,* and *stephensi* showed them to be quite similar to those of *albimanus*. When live, whole-mounted *Anopheles* larvae are viewed ventrally, two salivary ducts can be seen to enter the head and join to form a single median duct (fig. 1, MSD). This common duct runs ventral to the subesophageal ganglia and passes up the labium to empty on the antero-dorsal aspect of the prementum directly in front of the pharynx as described by

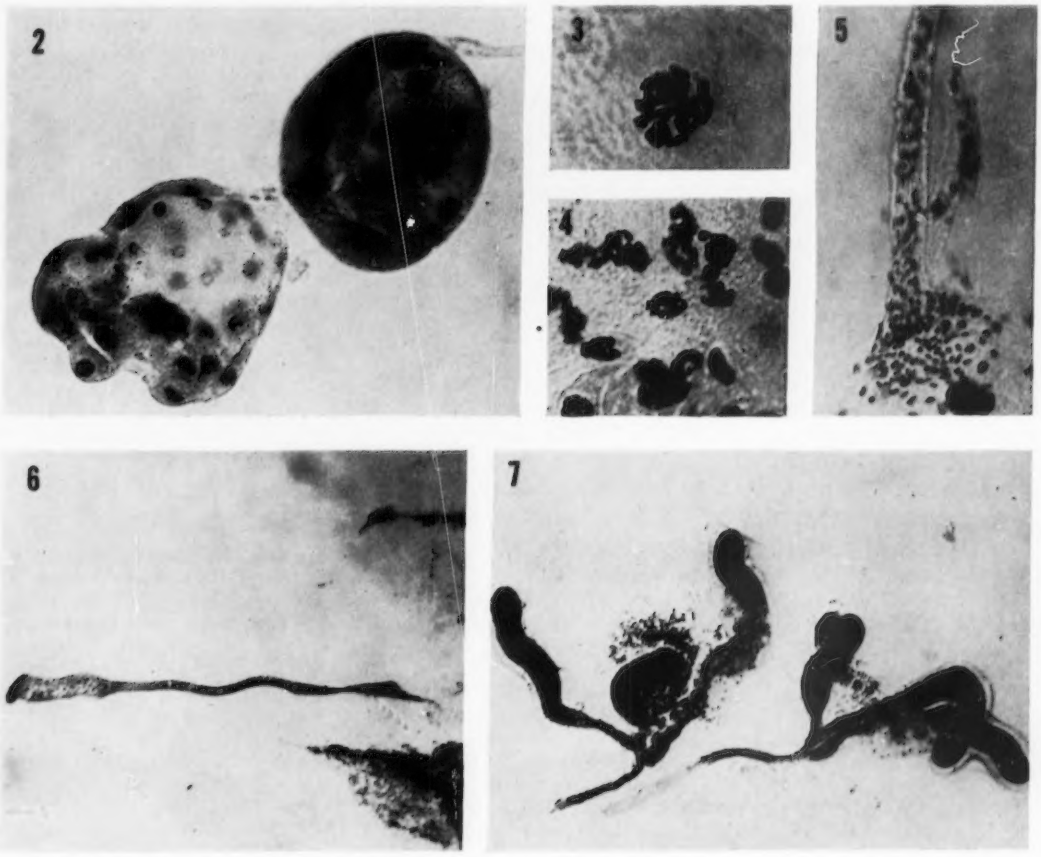

PLATE I, FIG. 2. A single salivary gland from a second stage *Anopheles albimanus* larva. Note the dark staining anterior and light staining posterior sacs. Feulgen stain. × 568.

FIG. 3. Typical large nucleus in anterior sac. Fourth stage larva. Feulgen stain. × 870.

FIG. 4. Typical nuclei in posterior sac. Fourth stage larva. Feulgen stain. × 870.

FIG. 5. Imaginal ring cells at the base of the slender salivary duct in fourth stage larva. Note absence of taenidial rings in the duct. Feulgen stain. × 870.

FIG. 6. Developing imaginal salivary gland in 20-hour old male pupa. Feulgen stain. × 210.

FIG. 7. Definitive imaginal salivary glands in 24-hour old female. Delafield's hematoxylin. × 75.

Farnsworth (1947). The salivary ducts in larvae do not have taenidial rings. Neither muscles nor nerves were found to be associated with the preimaginal salivary glands or their ducts in *Anopheles*. The glands also lack tracheae.

The larval salivary glands in *Culex pipiens* differ considerably from those in *Anopheles*. In *Culex* the proximal portion is elongated and cylindrical and made up of small cells, while the terminal sac is globular and made up of much larger cells. A conspicuous muscle is attached at the end of the terminal sac in *Culex*. In *Aedes aegypti* the salivary glands are cylindrical for three-fourths of their length and then become dilated towards the distal end. In *Aedes atropalpus* the entire salivary gland is elongated and cylindrical.

2. *Growth of the larval glands.*—Glands removed from newly hatched larvae are very minute, measuring about 60 microns in length. The anterior part is poorly developed and barely distinguishable from the salivary duct; even after staining it is difficult to distinguish its nuclei. The terminal sac is larger, has very distinct nuclei, and its lumen contains droplets. By the second day of the first stage, the anterior sac has become well-defined and its nuclei clearly distinguishable and of nearly the same size as those in the terminal sac. Banding of the chromosomes first becomes evident in late third stage larvae.

As with other dipterous larvae, the number of cells in the salivary glands of *Anopheles* was found to remain essentially constant throughout larval life, so that growth occurs solely through increases in cell size. This growth is shown graphically in figure 8. The log dimensions of the various portions are seen to be approximately linear with respect to age through the third stage. The glands reach their maximum size about the third or fourth day of the fourth stage and with pupation steadily decrease in size. The ventral nephrocyte chain, on the other hand, reaches its maximum size in the pupal stage (fig. 8) and its growth is linear through the fourth stage.

The amount that different portions of the salivary gland complex grew up through the third larval stage was calculated to obtain day to day as well as stage to stage growth rates (table 1). The differences between the growth rates of anterior and posterior sacs are not statistically significant. The nephrocyte chain, which is not destroyed during the early hours after pupation, has a significantly different growth rate from that of the salivary glands themselves (table 1). During larval life the anterior sac increases about 7 times in size, the posterior part of the gland increases roughly 5 times, and the salivary ducts enlarge 3 to 4 times. The ventral nephrocyte chain approximately doubles in width during larval life.

TABLE 1

GROWTH RATIOS FOR DIFFERENT PORTIONS OF THE LARVAL SALIVARY GLANDS OF *Anopheles albimanus*, ALONG WITH THE ASSOCIATED VENTRAL NEPHROCYTE CHAIN

PORTION MEASURED	GROWTH RATIOS THROUGH THIRD STADIUM	
	Day to Day Rate (geometric mean)	Stage to Stage Rate (geometric mean)[a]
Anterior sac		
length	1.22	1.82
width	1.22	1.82
nuclei	1.23	1.86
Posterior sac		
length	1.18	1.64
width	1.18	1.64
nuclei	1.21	1.77
Salivary duct width	1.15	1.52
Ventral nephrocyte chain	1.04	1.12

3. *Metamorphic events.*—While the salivary glands of the larva are growing in size, a series of less conspicuous but important events have been occurring in the cells destined to form the salivary glands of the adult. A ring of 12 to 15 minute cells at the anterior end of each larval gland becomes first clearly visible in the late first instar. The number of cells in this ring approximately doubles in each stadium until at last more than a hundred cells are found therein in fourth instars (fig. 5). They are tightly packed, very tiny cells with oval nuclei except for a few at the distal end which are larger and have round nuclei. Mitotic divisions were not observed in the imaginal ring cells.

When pupation occurs, the nuclei in the terminal sac of the larval gland degenerate rapidly and the whole portion diminishes in size (fig. 8). Nuclei in the anterior part of the larval gland degenerate less rapidly. Four to eight hours after pupation, the glands become

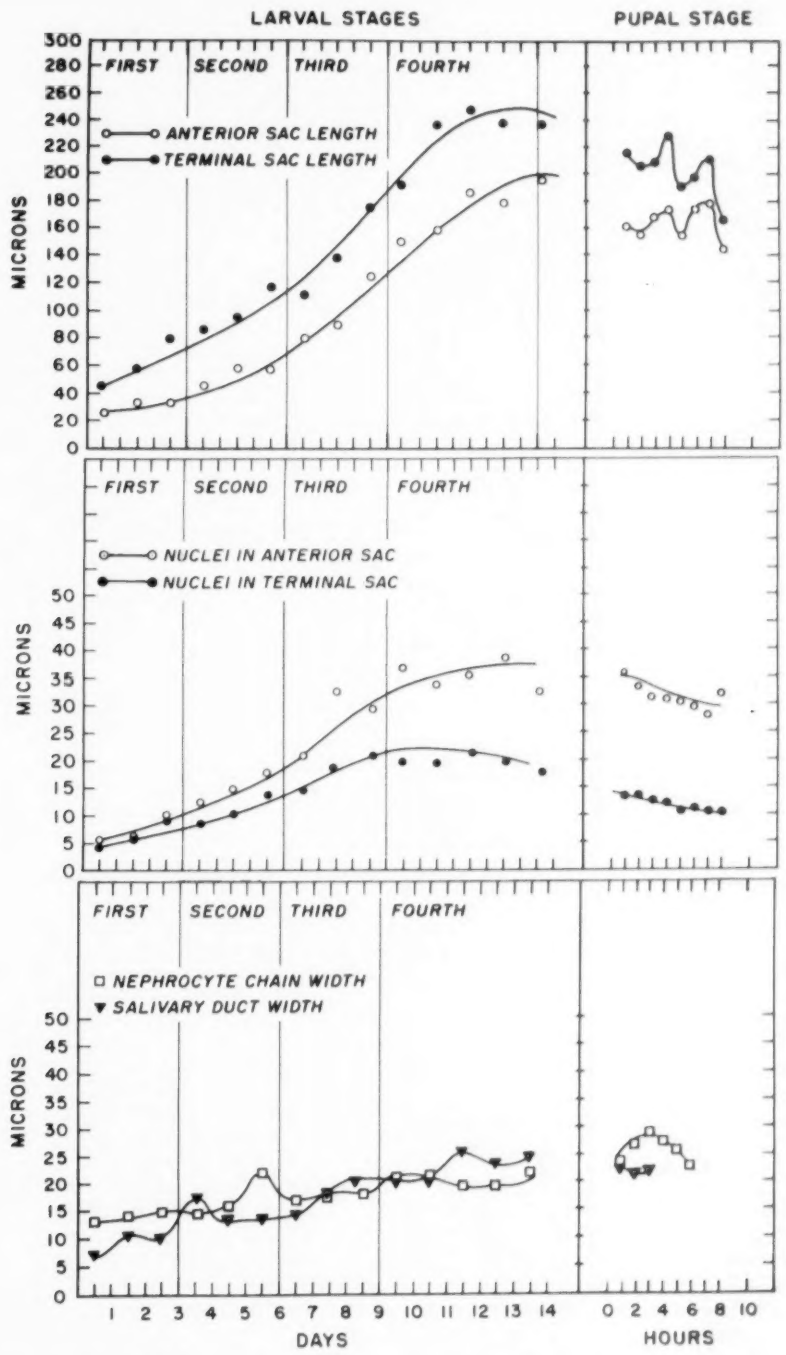

FIG. 8. The growth of different portions of the larval salivary glands and the ventral nephrocytes in *Anopheles albimanus*. Each point is the average of measurements taken from 10 to 25 larvae.

increasingly vacuolated, and their nuclei are found at the outer edges of the cells. Histolyzing glands were seen up to 20 hours of pupal life, hemocytes taking no visible part in their degeneration.

As these changes take place, the imaginal glands begin to differentiate. Approximately five hours after pupation, the imaginal ring in the male is separated from the larval glands in dissected material, and appears as a tiny one-lobed structure dilated at its distal end, apparently having its full complement of cells at this time (fig. 6). In the female pupa the imaginal ring differentiates into three finger-like prongs amidst the degenerating larval gland cells. At about the seventh or eighth hour of pupal life minute three-lobed glands separate from the larval glands in dissected material. The cells in the differentiating glands of the female at this developmental stage seem definitely fewer than those visible later on in the definitive adult.

Differentiation is completed chiefly during the early hours after pupation. The glands then become greatly elongated as the cells increase in size. The imaginal glands do not attain their full size and the middle acinus in the female does not completely differentiate until shortly *after* the emergence of the adult (fig. 7). Shortly before emergence, the lateral acini of the glands contain droplets.

DISCUSSION

The development of the salivary glands and the ventral nephrocytes in *Anopheles albimanus* beautifully illustrates three well-known concepts of growth and differentiation among the Diptera. (1) The larval glands grow through continuous and essentially linear increase in cell size, but the cells do not multiply. These glands reach their maximum size shortly before pupation and are rapidly destroyed during the early hours of metamorphosis. (2) The imaginal salivary gland discs grow during larval life primarily through cell multiplication. Although mitotic divisions were not observed in any of our preparations,[5] we assume that they do occur and suspect that all of the cells in the ring undergo mitosis rapidly and at the same time. If this speculation is correct the growth of these discs during larval life is a cyclic phenomenon. (3) Tissues like the ventral nephrocyte chain, which do not undergo profound metamorphosis, grow more slowly during the larval stages and so reach their maximum size in post-larval life, quite unlike strictly larval tissues.

Some interesting comparisons can be made between the morphology and the development of the salivary glands in *Anopheles* and *Drosophila*. In making this comparison we have used the detailed account of *Drosophila* salivary glands as given by Bodenstein (1950).

In *Drosophila* larvae the salivary ducts, which have taenidia, open into the pharynx itself, while in *Anopheles* the ducts have no taenidia[6] (as first shown by Imms, 1907) and empty in front of the opening into the pharynx. In *Drosophila virilis* the salivary glands are made up of 115 cells whereas in *Anopheles* the glands are composed of notably fewer cells (72 to 75). In *Drosophila* larvae the glands grow down as far as the second abdominal segment, while in *Anopheles* they are strictly confined to the thorax. The salivary glands of *Drosophila* appear as simple elongated sacs until the third instar (Bodenstein's stage 6), at which time anterior and posterior zones are recognizable. In *Anopheles* larvae, on the other hand, the salivary glands have two clearly defined regions from the first stage onwards. In the salivary gland of *Drosophilia*, Bodenstein states, ". . . there is never any sharp separation of anterior and posterior cells." In *Anopheles*, however, cells in the anterior and posterior portions are distinctly different as to size and nuclei and there is no intermediate zone of graduation. According to Bodenstein, "the anterior cells grow more slowly than the posterior cells" in *Drosophila*. In *Anopheles* no statistically significant differences between the growth rates of anterior and posterior cells could be demonstrated up through the third stage. In *Drosophila* the imaginal salivary gland ring appears first in the second instar (30 hour old larvae), while in *Anopheles* the ring is visible in the late first instar. In both *Drosophila* and *Anopheles* the posterior portion of the salivary gland degenerates before the anterior part during the early stages of metamorphosis.

The larval glands are probably more or less continuously secretory even in the absence of food for they do not diminish in size in *Anopheles* starved for several days.

It would be very interesting to know if both portions of the salivary glands in *Anopheles* larvae have distinctly different functions. The larger nuclei of the anterior sac suggest the possibility that this is the actively secreting portion. Perhaps the posterior sac is a reservoir. The anatomical differences noted between the salivary glands of the different species may provide a means of determining the answers to such questions.

SUMMARY

1. The paired salivary glands of *Anopheles albimanus* larvae have a spherical anterior portion of 12 to 15 polygonal cells with large nuclei and a larger terminal sac of 50 to 60 cells with smaller nuclei. No muscles, nerves, or tracheae were

[5]Ross (1939) also failed to detect mitotic divisions in the imaginal salivary gland ring in *Drosophila*.

[6]*Chaoborus* larvae also lack taenidial rings in their salivary ducts (Debauche, 1933).

found associated with these glands. A slender chain of ventral nephrocytes extends between the paired glands.

2. The larval glands grow only by increases in cell size. The growth rates of the different portions are essentially the same. The maximum size of the glands is reached shortly before pupation, after which they rapidly histolyze, the posterior portion degenerating before the anterior.

3. The imaginal salivary glands originate from a small ring of cells first visible at the anteriormost end of the larval glands in the first instar. The number of cells in this ring approximately doubles in each larval stage. As the larval glands begin to degenerate in the pupa, the ring cells differentiate into one-lobed glands in the male and three-lobed glands in the female.

4. The anatomy of the salivary glands in *Anopheles albimanus* is briefly compared with several other *Anopheles*, and with *Culex* and *Aedes* larvae.

ACKNOWLEDGMENTS

We wish to thank Mrs. Helen Louise Trembley Durkee for her encouraging interest in this work and for her kindness in supplying all of the species used and most of the facilities for the study. We gratefully acknowledge the stimulating advice concerning the preparation of this manuscript given us by Drs. J. B. Buck, M. L. Keister, and A. Glenn Richards. For statistical help we thank Mrs. Bernard Fox.

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EXTERNAL MORPHOLOGICAL DESCRIPTION OF THE LARVA OF EXOMALOPSIS CHIONURA COCKERELL, INCLUDING A COMPARISON WITH OTHER ANTHOPHORIDS[1, 2]

(HYMENOPTERA: APOIDEA)

JEROME G. ROZEN, JR.[3]

Included in this paper is a description of both the mature larva and the first instar of *Exomalopsis* (*Anthophorula*) *chionura* Cockerell. This represents the first relatively complete account of the mature larva of any member of the Exomalopsinae and is of special significance because it tends to clarify the relationship of this subfamily with others of the Anthophoridae. This relationship has been open to question until now (Michener, 1944, 1953).

The early stage larva is dealt with because it is different in appearance from the last and consequently may possess characters that would further refine the understanding of the phylogenetic affinities within the Anthophoridae. Unfortunately, too few young larvae of other subfamilies are available at the present time for this purpose, although there is sufficient material to clearly show that pronounced differences exist between the first instars of some of the groups.

The material employed in this study was

[1]The research for this paper was undertaken and the manuscript drafted while the author was associated with the California Insect Survey, University of California, Berkeley. The author's present address is Entomology Research Division, Agricultural Research Service, United States Department of Agriculture.

[2]Accepted for publication Jan. 29, 1957.

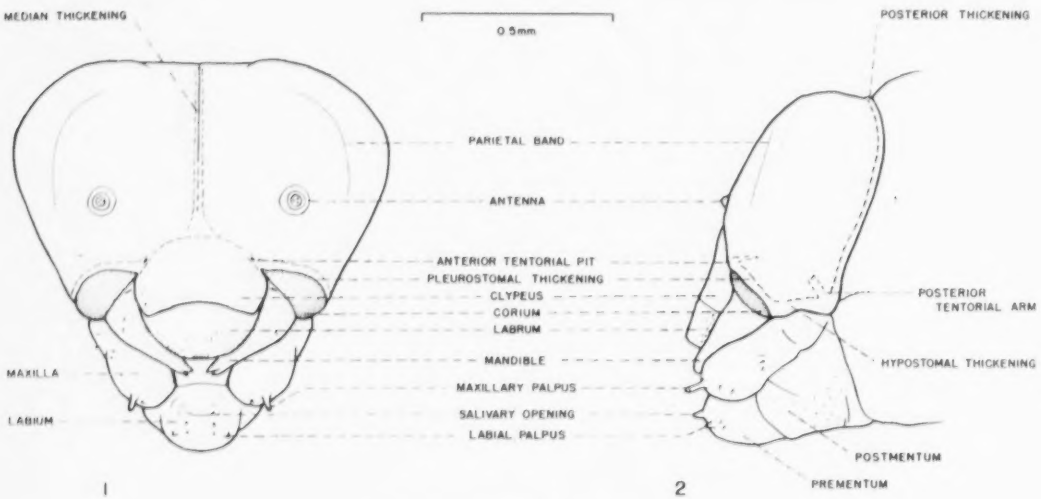
[3]I would like to express my appreciation to Professors E. Gorton Linsley and J. W. MacSwain for allowing me to examine the various stage larvae of *Melitoma euglossoides* Lepeletier, *Ptilothrix sumichrasti* (Cresson), *Nomada opacella* Timberlake, and *Melissodes timberlakei* Cockerell.

collected at Alpine Lake, Marin County, California, on August 12, 1955, by C. D. MacNeill and J. G. Rozen. It has been deposited in the collection of the California Insect Survey, University of California, Berkeley.

The study techniques and morphological terminology are those of Michener (1953). However, because the first instar is very delicate, both the head capsule and body were cleared in warm lactophenol and then examined in a droplet of the same agent. For purposes of comparison, the form of Michener's description has been adopted with only slight change.

MATURE LARVA

The following description refers to both predefecating and postdefecating (hibernating) individuals. As has been previously discussed



Exomalopsis chionura Cockerell

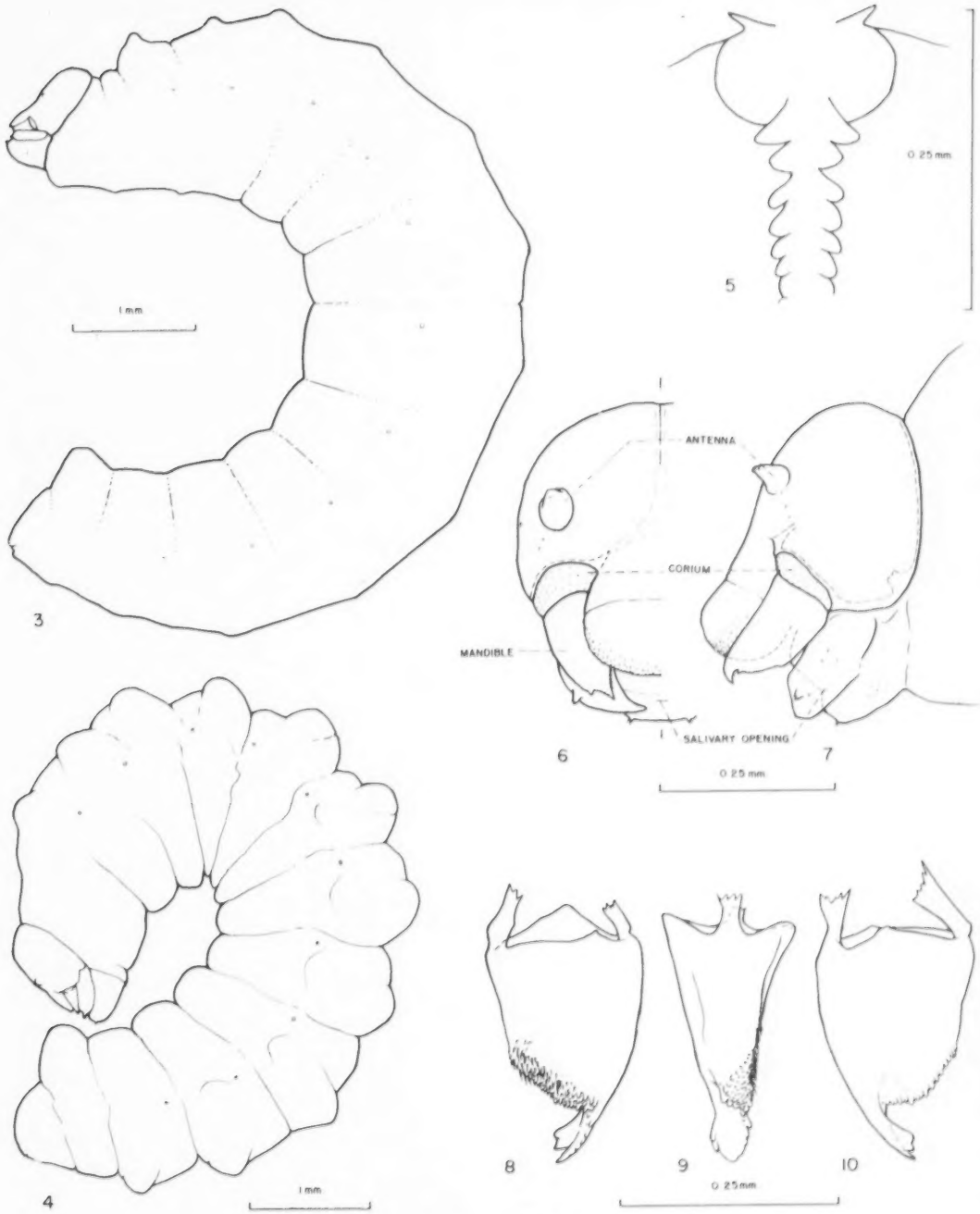
FIG. 1, frontal view of head of mature larva. FIG. 2, same, lateral view.

(Rozen, 1954: 203), the two forms are markedly dissimilar in appearance, although both represent the same instar. The differences pertain solely to the shape of the post-cephalic region of the body and are not associated with such structures as the cranium, mouthparts, or spiracles. As explained elsewhere (Rozen and MacNeill, manuscript) there is also a pronounced difference between the two forms with respect to behavior and physiology.

Description of Mature Larva

(Figs. 1-5, 8-10)

Head: Capsule and mouthparts with few widely scattered, minute setae. Posterior tentorial arms strong, arising from marginal thickening; anterior arms weaker. Marginal and pleurostomal thickening moderately well developed; hypostomal thickening more pronounced; epistomal thickening and corresponding suture moderately well developed laterad of anterior tentorial pits; median portion of thickening scarcely visible, being broad, thin, and ill-defined; corresponding suture obliterated. Longitudinal median thickening of head capsule pronounced, accompanied by more or less evident suture (epicranial); thickening becoming weaker toward epistomal thickening and broadly joining it; cleavage lines absent. Parietal band weak. Antennae feebly convex, each bearing distinct papilla which is at most as long as its diameter; papilla usually with three sensilla though occasionally with four. Labral tubercles weak, scarcely noticeable; labrum feebly emarginate apically (not noticeable on drawing), spiculate laterally, strongly so on epipharyngeal surface. Mandibles seen from above and below broad basally, narrow apically; apex bidentate, with upper tooth somewhat exceeding lower; upper margin broadly serrate apically, lower broadly bidentate (or perhaps tridentate on some); mandibular cusp, as seen from inside, oblique, forming pronounced inner subapical concavity; cusp strongly dentate; teeth also present on inner upper surface of mandible where they appear elongate, hair-like (lack of alveoli and the presence of a broad base, as revealed by microscopic examination under oil immersion, clearly demonstrate that these are not setae). Maxillae with palpi slightly subapical; maxillary apices bent mesad though not nearly as much as in the emphorines and anthophorines (this character is more obvious when seen in different view from



Exomalopsis chionura Cockerell

FIG. 3, lateral view of predefecating last instar. FIG. 4, lateral view of hibernating larva. FIG. 5, lateral view of spiracle of mature larva. FIG. 6, frontal view of head of early instar. FIG. 7, lateral view of same. FIGS. 8, 9, 10, dorsal, inner and ventral views of left mandible of mature larva.

that drawn) and bearing spicules on inner surface; palpi long, slender. Labium as seen from side very elongate, exceeding maxillae, clearly divisible into prementum and postmentum by transverse fold; labial lobe well developed, as seen from in front circular in outline, and bearing salivary opening at apex; salivary opening situated between two strongly projecting transverse sclerotized lips which are not as wide as distance between labial palpi; labial palpi slightly more than twice as long as wide; postmentum weakly spiculate.

Body: Form elongate, slender, in predefecating larva curved to form semicircle, in postdefecating one so curved that labium nearly or actually contacts eighth abdominal sternum. On predefecating larva, dorsolateral tubercles weak, especially on abdomen, intersegmental lines weak, and intrasegmental annulations absent; on postdefecating larva, dorsolateral tubercles more pronounced, intersegmental lines clearly defined, and intrasegmental annulations noticeable only on dorsum. Integument non-setose, that of lateral and dorsal portions of prothorax with relatively large spicules which become fewer posteriorly so that only few occur on mesothorax; posterior portion of body, particularly ninth and tenth abdominal segments, bearing small spicules; elsewhere body very weakly if at all spiculate (it is perhaps significant to note that the protruding ninth abdominal sternum is nonspiculate). Spiracles small, peritreme concave, primary tracheal opening collared; spiracular atria projecting above body wall. Ninth abdominal sternum prominent, projecting. Anus dorsally situated, surrounding area not sclerotized nor bearing ridges or spines.

It should be pointed out that the characteristics of the larva of *Exomalopsis chionura* coincide remarkably well with those listed by Michener (1953: 997) as being primitive. The only two features which do not agree are the non-setose body integument and the presence of a well defined inner subapical concavity on the mandibles. The condition of the antennal papilla seems to be somewhat intermediate. In a previous paper pertaining to adults, Michener (1944) states that, of the various anthophorids, the Exomalopsinae are clearly the most primitive.

COMPARISON WITH "*Exomalopsis*" *caerulea* FRIESE

The only other account of a larva of the subfamily is provided by Claude-Joseph (1926: 240) for "*Exomalopsis*" *caerulea* Friese and is accompanied by an illustration of the head and of the body. According to Michener (*in litt.*) this species is not an *Exomalopsis* but "is near *Tapinotaspis* and *Tapinotaspoides*". The specimen examined by Claude-Joseph was unquestionably a hibernating, post-defecating form as is evidenced by the description and illustrations. A translation of the text is as follows:

"They have a fusiform, cylindrical body, curved in a horse shoe, divided into segments doubly folded [probably referring to the annulations] on the dorsal surface (fig. 78). The head possesses a median depression. The appendages of the front [antennae] are clearly visible and are directed downward like short antennae. The convex labrum is produced into two anterior angles, each a chitinous point. The mandibles are conical, massive, and terminate in a darkened bevel. The cylindrical, abruptly truncate maxillae terminate in a little appendage. The lower lip is globulose, marked horizontally by a short and projecting scraper [lips of the salivary opening] at the base of which appear two pointed appendages."

Although in some instances it is not clear to what he is referring, a comparison of the larvae of *E. chionura* and "*E.*" *caerulea* can be drawn on the basis of his verbal description and illustrations. In cephalic aspect, the heads of both are generally triangular in outline and possess a dorsal median depression (more evident in *caerulea*). Although his description of the antennae is ambiguous, those of *caerulea* seem somewhat more pronounced than those of *chionura*. Whereas the labral tubercles of *caerulea* are projecting and prominent (and thus imparting an emarginated appearance to the apex of the labrum), they are scarcely evident in *chionura*. The apex of the mandibles of the two seems to be different. The truncate appearance of the maxillae of *caerulea* is probably caused by the apices being bent inward, a characteristic of *chionura*. The labial lobe of both is prominent and globulose and bears at its apex the somewhat short (compared with that of the emphorines and eucerines), strongly projecting lips of the salivary opening. Whereas he described the body form of *caerulea* as fusiform (also so illustrated), that of *chionura* appears more cylindrical. The intrasegmental annulations of *caerulea* are depicted as being more pronounced and at the same time his drawing indicates the absence of a strongly projecting ninth sternum (although this character may well have been overlooked).

It is difficult at this time to assess the full taxonomic (and phylogenetic) significance of these differences, although it is obvious that the condition of the labral tubercles, appearance of the mandibles, and length of the antennae can be regarded as denoting considerable taxonomic diversity. However, the dissimilarity in body shape and contour of the ninth sternum can probably be evaluated as major differences, in view both of the probable adaptive function of these features as found in *E. chionura* and of the degree of constancy with which they do or do not occur in the various subfamilies of the Anthophoridae.

COMPARISON WITH OTHER ANTHOPHORID GROUPS

The work of Michener (1953) and that of Linsley, MacSwain, and Smith (1956) permit a comparison of the larva of *Exomalopsis chionura* with those of other anthophorid bees. (Because of the incomplete knowledge of "*Exomalopsis*" *caerulea*, it is discussed only parenthetically when it is known to disagree with *E. chionura*.) As stated in the introduction, this procedure is of considerable value because it sheds light upon the phylogenetic relationship of the Exomalopsinae with the other members of the Anthophoridae (Anthophorinae of Michener).[4] It should first be stressed, however, that the conclusions based upon the following comparisons must be considered tentative until the larvae of more representatives of each subfamily can be studied.

EMPHORINAE: Considering first the pollen collecting subfamilies of the anthophorids, there is a strong resemblance between *Exomalopsis*, as represented by *chionura*, and the emphorine genera *Diadasia* Patton, *Melitoma* Lepeletier and Serville, and *Ptilothrix* Smith (including *Emphor*). Characters shared by them pertain primarily to body shape. All (but apparently not "*E.*" *caerulea*) possess an elongate post-cephalic region, protruding ninth abdominal sternum, and a dorsally situated anus. The first two characters presumably are adaptive for moving about the pollen mass during feeding, and the last, for plastering the fecal material against the cell wall (and cocoon in the case of *Exomalopsis chionura*) (Linsley, *et al.*, 1956; Rozen and MacNeill, manuscript). It is also of significance that the spiracles of all these groups possess an atrium without spines and a collared primary tracheal opening. These genera have certain similarities of the head capsule and mouthparts: weak parietal band; slender antennae; maxillae with apical portion bent inward (though less so in *Exomalopsis* but apparently more strongly in "*E.*" *caerulea*); salivary opening at apex of labial lobe; and salivary opening surrounded by projecting lips.

Exomalopsis, as represented by *chionura*, differs from these genera in a number of characters: triangular outline of head when viewed from the front; shorter antennae (apparently longer in "*E.*" *caerulea*); multidentate mandibular cusp; maxillary apices less strongly bent inward; labial lobe exceeding maxillae; salivary opening narrower, not equal to distance between labial palpi; and non-sclerotized and non-spined anal area of tenth abdominal segment.

Several characters which appeared at first to be potentially significant as a basis for phylogenetic interpretation now appear to be of no value at the subfamily level. Pronounced labral tubercles are found in both "*Exomalopsis*" *caerulea* and *Melitoma euglossoides*, whereas in *Exomalopsis chionura* and the other emphorine genera they are reduced. Although the spiracles of *Diadasia* and *Ptilothrix* (and *Emphor*) are large, those of *Melitoma* are small (Linsley, *et al.*, 1956, fig. 6), much like those of *Exomalopsis*. In view of the similar size of the spiracles of *Melitoma* and *Exomalopsis*, it is interesting to note the biological features held in common by them (Rozen and MacNeill, manuscript).

EUCERINAE: *Exomalopsis* shares certain characteristics with the genus *Melissodes* Latreille, the only eucerine of which the larva is known. The most pronounced are the denticulate condition of the mandibular cusp, the maxillae bent slightly inward, the elongate palpi, and the elongate salivary opening. These two genera ("*E.*" *caerulea* agrees with *Melissodes*) differ with respect to the body form, shape of the ninth abdominal sternum, spiracles, and position of the anal opening.

ANTHOPHORINAE[5]: A comparison of *Exomalopsis* with *Anthophora* reveals no features which are shared only by these two genera, and they differ not only in those characters by which *Melissodes* disagrees with *Exomalopsis*, but also in the mandibular dentition, palpal length, and condition of the salivary opening.

PARASITIC GROUPS: For the most part, there is but little resemblance between the larva of *Exomalopsis* and those of the nomadine-like parasitic bees (*i.e.*, Nomadidae of authors; the nomadine, ammobatine, epeoline, and holcopasitine[6] larvae of which are known). The two main points of similarity seem to be: the mandibular cusp of *Exomalopsis* and that of *Nomada* and *Holcopasites*[6] (but not of the other known larvae of this parasitic group) are dentate; and secondly the spiracles of most of these parasitic bee larvae possess both atria which rise above the body wall and a collar around the primary tracheal opening.

[4]In accordance with the practice of Linsley and his co-workers at the University of California, Berkeley, I am considering the Anthophorinae of Michener as being a distinct family. Consequently, his tribes are alloted subfamily status in this paper.

[5]Linsley, *et al.*, 1956, have suggested that *Xeromelecta californica* (Cresson) may actually be more closely related to the Emphorinae than the Anthophorinae on the basis of both biological characters and the dorsal position of the anus of the larvae. The following morphological features of the larvae can be added to these and seem to favor this conclusion: the relatively elongate antennal papillae, the salivary opening, the rather elongate palpi, the non-spinose atrial wall, and the presence of an atrial collar. It should be mentioned that while some of these similarities may be considered adaptive to the one biological characteristic of cocoon spinning, the position of the anus and the features of the spiracles can not be readily interpreted in this fashion. A major difference between the larva of *Xeromelecta californica* and those of the emphorines is the shape of the mandible.

[6]Referred to by Michener, 1953, as Neopasitini, *Neopasites*.

Although the antennal papillae of *Exomalopsis* are somewhat reduced and the salivary opening is slightly narrowed (*e.g.*, compared with the emphorines), it is open to question whether or not these modifications can be interpreted as reflecting phylogenetic relationship. Other characteristics of the larvae of *Exomalopsis* are decidedly unlike those of the nomadine-like bees.

From a phylogenetic (and taxonomic) viewpoint, the morphology of the mature larva of *Exomalopsis* (and to a somewhat lesser degree, of "*E.*" *caerulea*) strongly suggests that the Exomalopsinae are closely related to the Emphorinae (and *Xeromelecta*, see footnote 5), a conclusion which is also indicated on biological grounds (Rozen and MacNeill, manuscript). However, there are enough differences in the morphology of the immature stages and of the biology, for these two groups to be considered distinct subfamilies (at least until other exomalopsine genera can be studied).

On the basis of a single larval representative of the Eucerinae, the exomalopsines and eucerines would seem to be somewhat less closely affiliated, and the relationship between the anthophorines and exomalopsines can be regarded as being even more distant on the grounds of their known biology and the morphology of the larvae.

Although Michener (1944) considers the Exomalopsinae and the nomadine-like parasitic bees to be closely related on the basis of the morphology of the adults, there are only a few morphological characters of the larvae and but little biological data to support this belief. If there is a true close relationship, it must be assumed that in the course of becoming adapted to their parasitic way of life and to the environment of the hosts, the nomadine-like parasites have undergone rapid change, so that their larvae bear little resemblance to the original exomalopsine-like stock. This possibility, however, is consistent with present day evolutionary knowledge.

FIRST INSTAR

The following description of *Exomalopsis chionura* is based upon the first instar, just after it has commenced to feed. Whereas the head is drawn from both a cephalic and lateral view, the post-cephalic region has not been depicted because of its relatively simple form.

Description of First Instar

(Figs. 7, 8)

Head: Capsule and mouthparts with few widely scattered, minute setae. Posterior tentorial arms moderately strong, arising from marginal thickening; anterior arms somewhat weaker. Posterior thickening of head capsule moderately well developed; hypostomal thickening more evident than posterior thickening; pleurostomal thickening weak, scarcely noticeable; lateral portions of epistomal thickening weak but broadly uniting with pleurostomal thickening; median portion of epistomal thickening between anterior tentorial pits scarcely evident. Longitudinal median thickening of head capsule scarcely evident; apparently broadly united with median portion of epistomal thickening; cleavage lines absent. Parietal band apparently absent. Antennae pronounced, conical, bearing sensilla at summit. Labral tubercles absent; labrum large, spiculate apically and laterally but smooth on epipharyngeal surface. Mandibular corium (unlike in mature form) spiculate; mandibles stout, sharply pointed apically, with upper and lower edges serrate apically and with lower edge bearing subapical tooth (corresponding to lower apical tooth of mature form); inner subapical concavity not as pronounced as in mature larva; cusp dentate, but not as densely so as in mature form; elongate, hair-like teeth absent. Maxillae with palpi distinctly subapical; apices elongate, bent inward, pointed, and without spicules; palpi moderately short. Labrum as seen from sides not elongate and not visibly divided into prementum and postmentum; labium not produced apically into a lobe; palpi shorter than those of maxillae; salivary opening a subapical, short, transverse slit without lips.

Body: Form slender, elongate, cylindrical, nearly straight. Dorsolateral tubercles and intrasegmental annulations absent, and intersegmental lines evident. Integument non-setose but conspicuously spiculate (or muricate) over entire body; anal area without spines. Spiracles much modified compared with mature form; atrium extending little if at all above body surface; peritreme flat; atrium shallow (though always shallow, there seems to be some variability within an individual with respect to this character); atrial wall apparently roughened although no definite spines noticeable; primary tracheal opening simple, without spines or collar; subatrium simple, not annulated. Ninth abdominal segment with sternum not projecting but enlarged so that segment equal in diameter to preceding, thus imparting somewhat truncate appearance to posterior end of larva; tenth segment small, with dorsally situated anus.

It is interesting to note that the lips of the salivary opening are absent, the labial lobe is missing, and the maxillary and labial palpi (but not the antennae) are much reduced, compared with those of the mature larva. Thus it is indicated that the modifications of these structures (though not the antennae) which are found in the mature larva are adaptations for cocoon construction, as suggested by Michener (1953).

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RESPIRATORY METABOLISM OF HOMOGENATES DURING THE EMBRYONIC DEVELOPMENT OF THE MEALWORM, TENEBRIO MOLITOR LINNAEUS, WITH ADDED SUBSTRATES AND INHIBITORS[1]

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Ludwig and Barsa (1955) compared the activity of the succinoxidase system with the rate of O_2 consumption during the egg stage of the mealworm, *Tenebrio molitor*. They found that enzyme activity remained constant during the first half and increased rapidly during the last half of this stage. Oxygen consumption, however, was very low in newly laid eggs. It increased rapidly during the first 24 hours and thereafter followed the same relative changes as did enzyme activity.

In the present study, various substrates and inhibitors of the succinoxidase system were added to homogenates of the mealworm during each day of the egg stage at 30°C., and readings on O_2 consumption were made to determine the relative importance of components of this system.

MATERIALS AND METHODS

Eggs of the mealworm, laid in white flour, were collected daily so that when obtained they were always less than 24 hours old. They were placed in a desiccator, the base of which contained a saturated solution of NaCl (relative humidity, 75 percent) and were incubated at 30°C. At the desired stage, they were homogenized for one minute with a motor driven glass homogenizer in 0.03 molar phosphate buffer adjusted to a pH of 7.4. Readings on the O_2 consumption of 5 percent homogenates with added substrates and inhibitors were made over a 2-hour period in Warburg constant volume manometers at 30°C., according to the method outlined by Umbreit, Burris and Stauffer (1945). Throughout this period the manometers were rocked horizontally 100 times per minute. The substrates, sodium succinate and cytochrome *c*, were added singly and together to the homogenate. The inhibitors, KCN, sodium malonate, alcohol, or DDT in alcohol, were added singly to homogenates containing sodium succinate and cytochrome *c*. All solutions were made in 0.03 molar phosphate buffer at a pH of 7.4. In each experiment, the thermobarometer contained test solutions except the tissue homogenate. The final concentrations in the manometer flasks were:

(a) M/9 sodium succinate,
(b) 0.6×10^{-4} M cytochrome *c*,
(c) 10^{-4} M KCN,
(d) M/9 sodium malonate,
(e) 1.25 percent ethyl alcohol,
(f) 10^{-3} M DDT in 1.25 percent ethyl alcohol.

The DDT was prepared by dissolving the crystals in 5 ml. of ethyl alcohol and adding this solution to 95 ml. of phosphate buffer. Cyanide inhibition was measured by the method of Robbie (1946).

OBSERVATIONS

The effects of added substrates and inhibitors on the O_2 consumption of 5 percent homogenates are shown in figure I. The graphs show that neither sodium succinate (Graph C) nor cytochrome *c* (Graph E) significantly increased the respiratory rate above that of the unfortified homogenate (Graph D). However, when both were added, the rate was approximately doubled throughout the embryonic period (Graph F). The addition of KCN (Graph A) or of sodium malonate (Graph B), reduced the rate below that of the unfortified homogenate. KCN was a more effective inhibitor than sodium malonate. Since the O_2 uptake of the unfortified homogenate increased during the latter part of embryogenesis, and with each of these inhibitors it remained

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relatively constant, the inhibitors were more effective during this period.

Figure 2 (Graph A) illustrates the effects of adding DDT and alcohol to 5 percent homogenates containing sodium succinate and cytochrome *c*. The respiratory rate of homogenates with DDT in alcohol was similar to that obtained with KCN (figure 1, Graph A). It increased slightly at the beginning of the embryonic period and

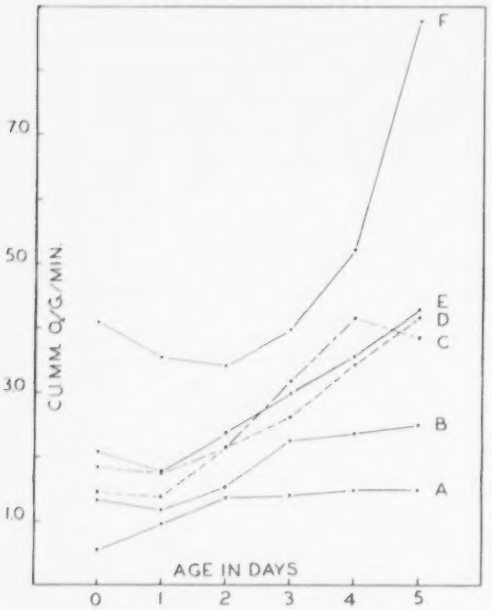

FIG. 1.—O_2 consumption of 5 percent homogenates during embryonic development. Graph A, homogenate with cytochrome *c*, sodium succinate and KCN; Graph B, homogenate with cytochrome *c*, sodium succinate and sodium malonate; Graph C, homogenate with sodium succinate; Graph D, unfortified homogenate; Graph E, homogenate with cytochrome *c*; Graph F, homogenate with both cytochrome *c* and sodium succinate.

then remained relatively constant throughout the remainder of the egg stage. The O_2 consumption of the control (homogenate with 1.25 percent alcohol, Graph B) indicates a strong inhibitory effect of alcohol. The alcohol not only eliminated all of the respiration induced by the addition of cytochrome *c* and succinate but lowered the rate of O_2 consumption below that of the unfortified homogenate. Since the respiratory curve obtained with alcohol rose progressively during the latter part of the egg stage, while that with DDT in alcohol remained relatively constant, the effect of DDT was much greater during the latter part of the embryonic period.

DISCUSSION

Ludwig and Barsa (1957) found that the addition of either sodium succinate or of cytochrome *c* to 5 percent homogenates during the metamorphosis of the mealworm produced a considerable increase in the rate of O_2 consumption of prepupae and pupae. Bodine, Lu and West (1952) working with the grasshopper, ***Melanoplus differentialis***, found that the addition of sodium succinate to homogenates increased O_2 uptake 300 percent in diapausing, and 140 to 150 percent in post-diapausing embryos. However, with mealworm eggs neither sodium succinate nor cytochrome *c* produced a significant increase in respiration. Since the addition of either substrate has no effect, but addition of both enhances respiration, the concentration of either substrate is a limiting factor. Therefore, it appears that the enzymes of the succinoxidase system are present in excess throughout the embryonic period of this insect.

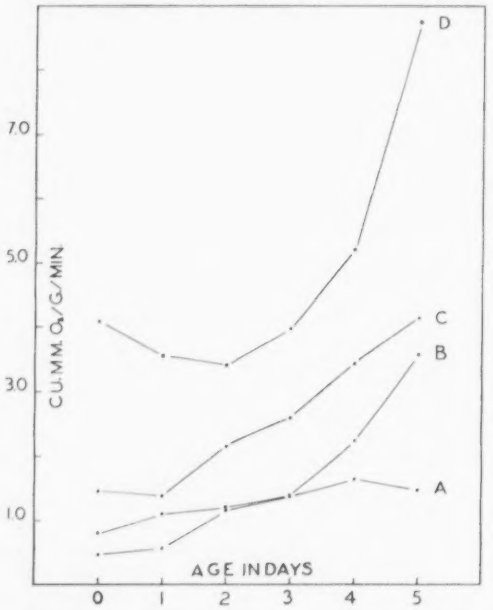

FIG. 2.—O_2 consumption of 5 percent homogenates of mealworm eggs with added substrates and inhibitors. Graph A, homogenate with cytochrome *c*, sodium succinate and 10^{-3} M DDT in 1.25 percent ethyl alcohol; Graph B, homogenate with cytochrome *c*, sodium succinate and 1.25 percent ethyl alcohol; Graph C, unfortified homogenate; Graph D, homogenate with cytochrome *c* and sodium succinate.

In mealworm pupae, KCN and sodium malonate eliminated nearly all of the respiration of homogenates induced by the addition of sodium succinate and cytochrome *c*, but none of the endogenous metabolism (Ludwig and Barsa, 1957); however, in the egg these inhibitors eliminated a considerable amount of the latter. They were more effective at the end of the embryonic period due to the increase in activity of the succinoxidase system.

Ethyl alcohol (1.25 percent) had a narcotic effect reducing the O_2 consumption of egg homogenates. In the larva, Ludwig and Barsa (unpublished) found that with 1 percent homogenates containing sodium succinate and cytochrome *c*, 10 percent alcohol produced an inhibition of 56 percent, 5 percent alcohol of 11 percent, while 1 percent alcohol produced a slight increase in respiration. In the pupa (Ludwig and Barsa, 1957), 1.25 percent alcohol increased the respiratory rate of 5 percent homogenates, but the same concentration of alcohol was ineffective with 1 percent homogenates. Thus it appears that a low concentration of alcohol has a stimulating effect on O_2 consumption. It may possibly be used as a substrate. However, as the concentration of homogenate was decreased, thus reducing enzyme activity in relation to the amount of alcohol present, the narcotizing effect of the alcohol became more pronounced. This effect decreased in the 4- and 5-day egg, probably due to the concomitant increase in the activity of succinic dehydrogenase (Ludwig and Barsa, 1955). DDT in alcohol appears to produce complete inhibition of cytochrome oxidase in egg homogenates since the respiratory curve with this poison was almost identical with that obtained with KCN. Complete inhibition of cytochrome oxidase was also obtained by Morrison and Brown (1954) using very dilute homogenates of cockroach muscle.

SUMMARY

1. The effects of adding substrates and inhibitors on the O_2 consumption of 5 percent homogenates were determined throughout the egg stage of the mealworm at 30°C.

2. The addition of either cytochrome *c* or sodium succinate failed to increase respiratory rate. However, when both were added it was increased to approximately that of the intact egg.

3. The inhibitors, KCN, sodium malonate and DDT, when used singly, eliminated all of the O_2 consumption produced by the addition of the substrates and a great deal of the endogenous respiration. They were most effective during the latter part of embryogenesis.

4. Ethyl alcohol (1.25 percent) reduced respiratory rate. However, its narcotic effect diminished towards the end of the embryonic period.

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ANNOTATED CATALOGUE OF AFRICAN GRASSHOPPERS, by H. B. JOHNSTON. With a preface by B. P. Uvarov. Anti-Locust Research Centre. Cambridge University Press, American Branch: 32 East 57th St., New York 22. 1957. xxii+833 pp. $18.50. (Cloth bound, 26 cm.)

There is no need to stress the value of a well prepared systematic catalogue, especially when the area covered is an entire continent and the taxonomy of the group involved needs revisionary study. In this case the group is of great economic importance also, and, as new regions of Africa are developed agriculturally, poorly known and even undescribed grasshoppers are becoming serious pests. Accordingly, heartiest commendations and thanks are due Mr. Johnston as well as the sponsoring organization. For Orthoptera, no catalogue of this stature has appeared since Kirby's world catalogue of 1904–1910.

The stated objective of the author was to bring together a complete and usable index to work dealing with African grasshoppers (Acridoidea), minus that dealing with the non-systematic aspects of five migratory species (locusts) on which the economic literature would have been unwieldy for this volume. While a complete coverage of literature through 1953 was the aim, at least five important 1954 papers also are included among the 981 publications cited in the bibliography.

No new synonymy or other systematic matter has been introduced, and it is frankly stated that the catalogue is not intended to be revisionary in character because so much basic work on African Acridoidea remains to be done. So strictly has the author avoided bringing in new material that in at least one case (*Pieltainidia*, p. 9) no genotype has been designated, and infra-specific categories are enumerated as they now stand in the literature. In the genus *Dictyophorus*, for example, species, subspecies, varieties, straight trinomials, and forms all are listed. In a few cases the latest classification of the Acridoidea, by Dirsh (Trans. Ent. Soc. London *108*: 223–356, 1956) shows an arrangement (family rank for the Lathiceridae and Charilaidae, for instance) different from that used in the present catalogue.

Africa is rich in grasshoppers, with 499 genera, 2,001 species and an additional 226 infra-specific named entities listed as valid in the catalogue. About 10 percent of the genera and 6 percent of the species were described during 1951–54, and important additions have been made since 1954. (In the United States and Canada about 130 genera, 505 species and 100 additional subspecies are now known.)

There is no doubt that this catalogue will be a tremendous stimulus and aid to the further study of African grasshoppers, as well as a challenge to workers in other groups.

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VARIATIONS IN MEGASTIGMUS FROM ROSE HIPS (TORYMIDAE, HYMENOPTERA)[1]

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INTRODUCTION

The two known species of *Megastigmus* from rose hips afford an unusually favorable group for a study of intraspecific and interspecific variation in size and color of the adults. They are very closely related (Milliron, 1949, p. 293), and have very similar habits and development, yet show striking differences as to the range of variation in size and color and also the numerical ratios of the sexes. The American form, *Megastigmus nigrovariegatus* Ashmead, and particularly the male, varies extremely in the percents of dark color, i.e., brown to black versus yellow pigmented areas on the body, and apparently comprises equal numbers of males and females. By contrast, the European species, *M. aculeatus* (Swederus), now known to occur also in Japan, China and the United States of America, shows, in my reared series, comparatively little range in color and size, and is predominantly female.

MATERIALS AND METHODS OF STUDY

In the course of my work on The Rose Hip Community, 1943–1953, I reared more than 8,000 adults of *nigrovariegatus* from many species of roses and localities of North America, and 1,076 of *aculeatus* from a few rose forms growing in North Carolina, New York, Ohio and Illinois. Data pertinent to the actual numbers, sources and years of the several acquisitions are given in tables 1 and 2.

Method of study. With reference to size, the specimens were divided arbitrarily into three groups, namely (1) small, that measured 1.5 to 2.2 mm. long; (2) medium size, 2.3 to 2.8 mm. long, and (3) large individuals having a length of 2.9 to 3.5 mm. Preliminary experience showed it was desirable to estimate the lengths with the eye aided by a binocular instead of measuring them with calibrated instruments. Use of the latter proved to be both cumbersome and unrealistic due to the many varied postures in which the specimens chanced to be mounted on the paper points.

As to color, the specimens were divided into four groups on the basis of the percents of brown or black versus yellow areas present on the dorsa of the head, thorax and propodeum. Other surfaces of the bodies were not considered for the reason that they were sometimes obscured by the paper points or the appendages. Group 1 embraces the chalcids having 1 to 25 percent of these dorsa dark; group 2 includes specimens 26 to 50 percent dark; group 3, those with 51 to 75 percent; and group 4, chalcids having those areas 76 to 100 percent dark. A fixed percental value was assigned to each of the several dorsal areas, as follows: vertex of the head, 20 percent; pronotum, 20 percent; mesonotum, 40 percent; and the metanotum and propodeum combined, 20 percent. Each individual was then placed in a percental group on the basis of the total percents of dark color on these dorsal areas (tables 1 and 2).

The vertical sequence of the nine samples of *nigrovariegatus* represented in table 1 coincides with the percents of large males. For example, the lot reared from *Rosa acicularis* at Eaglesnest, Minnesota, contains the maximum, or 27.65 percent large specimens and is, accordingly, placed in the uppermost horizontal space within the table. At the bottom occurs the lot of 243 males from *R. blanda* and the related *R. macounii*, which embraces no large males at all. The table as a whole is concerned with a grand total of 6,463 individuals which are 3,294 males and 3,169 females.

VARIATIONS IN *Megastigmus nigrovariegatus*

In size. The length of the 6,463 *nigrovariegatus* ranged from 1.5 to 3.5 mm., the males being generally slightly smaller than the females. In a sample of this magnitude, the variation from smallest to largest is continuous and regular, the intermediates constituting the large majority, as the following figures, based on males and females combined, show. Here 17.0 percent are small, 6.0 percent large and 77.0 percent medium in size. As to sex, the sample embraces 22.25 percent small males, 6.11 percent large, and 71.64 percent medium-sized males. Similarly, the females are 12.10 percent small, 5.24 percent large, and 82.66 percent medium in size. Incidentally, it appears from these values that the measurements adopted as a basis for the three categories of size should have been modified in favor of the "large" group in order to secure a more balanced percental distribution.

In Color (pl. I, figs. 1–7). *M. nigrovariegatus* shows a striking intersexual difference in the areas of dark and yellow colors. Within the series of 3,294 males examined (table 1), the percents of black varied from 0 to 100, whereas the majority of the 3,169 females are only 0 to 25 percent dark,

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and none exceed 51 percent. For particulars as to variation in color, see table 1.

Flame red adults. In the sample of 6,463 *nigrovariegatus*, I found 52 individuals of a fiery or flame red color. All the body regions showed this fiery red, but it was most intense on the mesonotum, and occurred on both males and females. They originated in hips of *Rosa blanda*, *carolina*, *virginiana* and *rugosa* from Chetek, Wisconsin, and Illinois, and in different years.

It is barely possible that this flame color was due to the action of cyanide in killing jars. However, the large majority of my reared materials was exposed to this gas without such effect. Since the flame color was most extreme among series whose mesonota are orange-yellow, it may represent merely an intensification of the pale orange pigment frequently present in the species.

from hips grown at North Carolina and Fox Ridge Park, Illinois. By comparison, the six samples of females, totalling 1,045 individuals, gave 51.14 to 100 percent individuals of medium size, i.e., 2.3–2.8 mm. long. However, the range in size of the females as indicated in the table is actually more limited than these percents suggest, for the majority of the long series of 834 from *Rosa virginiana* at Fox Ridge Park fall near the borderline between medium and small. Only 1.20 to 5.00 percents of the females in five local samples rank as "large," i.e., 2.9–3.5 mm. long. This very small percent of large females, on the one hand, and the minority of small ones, or 1.96 to 44.06, on the other, signifies that, with reference to variation in size, the females of *aculeatus* are decidedly more uniform than their counterparts of *nigrovariegatus*.

In color (pl. I, figs. 8, 9). Consideration of

TABLE 1

STATISTICS OF VARIATION IN *M. nigrovariegatus*

SOURCES	ROSES	SEXES	INDIVIDUALS PER SAMPLES	RATINGS BASED ON SIZE IN PERCENTS			RATINGS BASED ON AMOUNTS IN BLACK, IN PERCENTS			
				Small	Medium	Large	1–25	26–50	51–75	76–100
Eaglesnest, Minnesota	*acicularis*	♂♂—>	217	00 9	71 4	27 7	00 0	29 4	50 2	20 3
		♀♀—>	314	00 0	83 1	16 9	3 2	96 5	00 3	00 0
Poynette and Madison, Wis.	*arkansana*	♂♂—>	95	14 7	68 4	16 8	20 0	69 5	10 5	00 0
		♀♀—>	100	17 0	66 0	17 0	100 0	00 0	00 0	00 0
Maine, Wisconsin and Illinois	*rugosa*	♂♂—>	531	30 0	54 8	15 2	11 7	44 4	34 5	9 4
		♀♀—>	874	12 0	79 6	8 4	87 1	12 8	00 1	00 0
Alaska	*acicularis*	♂♂—>	148	10 1	80 4	9 5	00 7	72 3	25 0	2 0
		♀♀—>	145	1 4	82 8	15 9	00 0	100 0	00 0	00 0
Chetek, Wis.	*blanda* and *carolina*	♂♂—>	617	5 9	92 5	1 6	11 4	78 4	9 3	00 9
		♀♀—>	425	1 2	98 8	00 0	92 5	7 5	00 0	00 0
Missouri, Illinois and Wisconsin	*carolina*	♂♂—>	1068	25 8	72 6	1 6	41 9	53 4	4 0	0 7
		♀♀—>	889	15 0	85 0	00 0	99 9	00 1	00 0	00 0
Homeworth, Ohio	*palustris*	♂♂—>	162	55 6	43 8	0 6	58 0	39 5	2 5	00 0
Urbana, Illinois		♀♀—>	104	32 7	67 3	00 0	98 1	1 9	00 0	00 0
Orono, Maine	*virginiana*	♂♂—>	213	44 1	55 4	0 5	18 8	63 9	16 4	0 9
Urbana, Illinois		♀♀—>	189	40 7	59 3	00 0	86 8	13 2	00 0	00 0
Saskatoon, Can.	*blanda*, incl.	♂♂—>	243	19 8	80 3	00 0	1 2	65 9	26 8	6 2
Ottawa, Can. Eaglesnest, Minn. Solon Springs, Wis.	*Macounii*	♀♀—>	129	7 8	92 3	00 0	28 7	71 3	00 0	00 0

VARIATIONS IN *Megastigmus aculeatus*

The following statement regarding variations in size and color of *M. aculeatus* is based largely on a sample of 1,076 adults reared at Urbana from hips of roses that originated in places named in table 2.

In size. As stated above, *M. aculeatus* is predominantly female, this sex occurring in the ratio of 34.7 to one male in the sample treated here. Similar disproportional numbers are reported also by Hoffmeyer and Milliron. If the 31 males of my sample are typical of their sex, they average somewhat smaller than the females, as is indicated by the 93 and 75 percents of "small" males, i.e., 1.5–2.2 mm. long, reared

(a) published descriptions and (b) my reared series make it clear that *M. aculeatus* is subject to a more limited range of variation in color than is its congener, *M. nigrovariegatus*. This is true of both the males and females. Yet *M. aculeatus* does show noteworthy departures from the typical *M. aculeatus aculeatus* of Hoffmeyer (1929). The latter investigator considered certain Japanese materials from *Rosa multiflora* as worthy of varietal status on the basis of color—a form he named *M. a. nigroflavus*. Moreover, I have other color variants which do not conform to Hoffmeyer's description of *nigroflavus;* these suggest the possibility that further departures from the typical form may be found as we obtain

specimens from additional species of roses and ecological situations as the species continues its spread into now unoccupied areas. Its range of color may prove to be so broad as to be almost or quite continuous, and therefore render the recognition of color varieties as untenable as in *M. nigrovariegatus*. However, the nature of the variation found in my series suggests it will prove less fluent or extreme than that already demonstrated in *nigrovariegatus*.

Concretely, my series of *aculeatus* (table 2) may be divided into two fairly distinct lots according to the relative amounts of black and yellow in the pattern. The females reared from hips that originated in North Carolina, Geneva, New York, and at East Liberty and West Lafayette, Ohio, form the lighter group. This shows 11 to 17 percent of black on the dorsal side (fig. 8), which is a very narrow range of variation compared with the 1 to 51 percent of black surfaces on females of *nigrovariegatus*. In contrast with the lighter series, the females of *aculeatus* obtained from Kickapoo and Fox Ridge Parks, located near Danville and Charleston, Illinois, respectively, show 36–54 and 32–43 percent of black-pigmented surfaces (fig. 9).

TABLE II

STATISTICS OF VARIATION IN *M. aculeatus*

SOURCES	ROSES	SEXES	INDIVIDUALS PER SAMPLES	RATINGS BASED ON SIZE IN PERCENTS			RATINGS BASED ON AMOUNTS, OR PERCENTS OF BLACK			
				Small	Medium	Large	1–25	26–50	51–75	76–100
Ashe County, N. Car.	*eglanteria* L. (*rubiginosa* L.)	♂♂	15	93.3	6.7		100			
		♀♀	102	1.9	93.0	5.0	100			
East Libery, Ohio	*Rosa* sp.	♂♂	0							
		♀♀	36	38.9	59.1	2.0	100			
West Lafayette, Ohio	*eglanteria*	♂♂	0							
		♀♀	28	44.1	54.7	1.2	100			
Geneva, N. Y.	*Rosa* sp.	♂♂	0							
		♀♀	24		97.0	3.0	100			
Kickapoo Park, Ill.	*eglanteria*	♂♂	0							
		♀♀	21		100.0			95.2	4.8	
Fox Ridge Park, Ill.	*virginiana*	♂♂	16	75.0	25.0			100.0		
		♀♀	834	12.6	82.9	4.5		100.0		

QUALITATIVE VARIATIONS IN COLOR

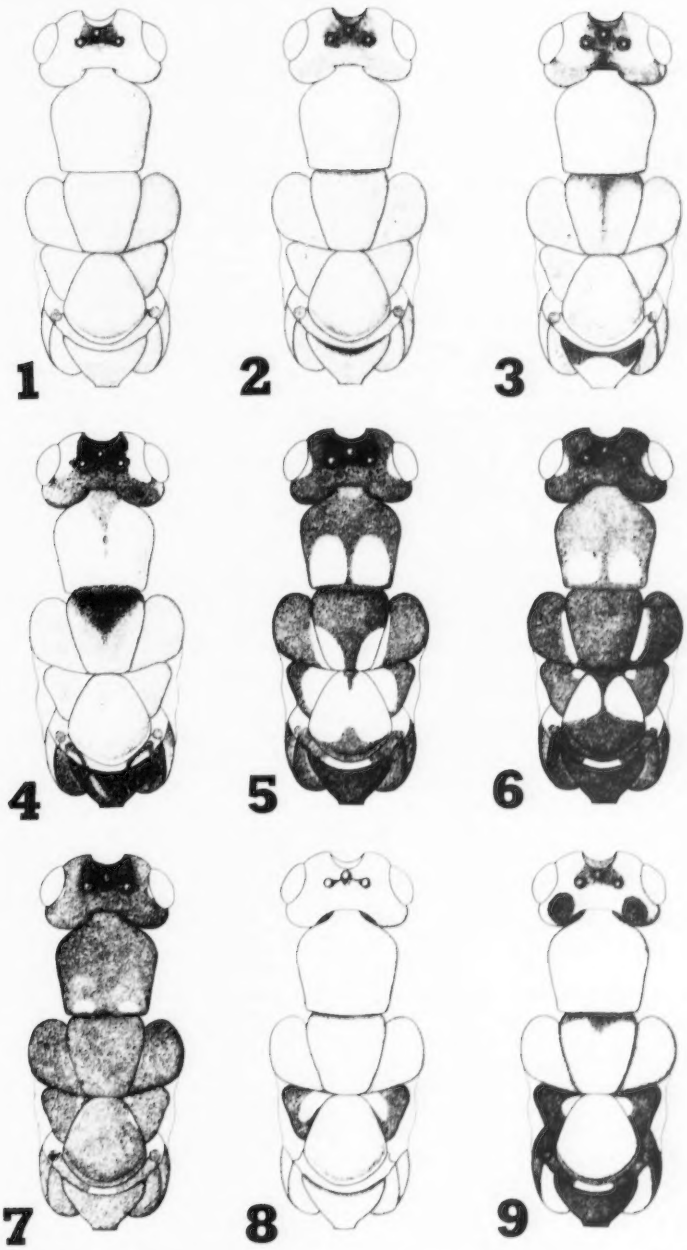
Not only quantitative but qualitative differences distinguish *M. aculeatus* and *nigrovariegatus*. The atures that characterize *aculeatus* are its bright orange-yellow patches which usually contrast sharply, with precise border lines, against the solid brown to black spaces. By contrast, in the instance of *nigrovariegatus*, the black pigment invading the yellow areas tends to obliterate the border lines between yellow and black, thereby producing many intergrades in shade and quality of light and dark colors in the transitional zones.

The basic color. Two observations indicate that yellow, rather than brown or black, is the basic color on both *M. aculeatus* and *nigrovariegatus*. First, yellow occurs on the entire bodies of the smaller individuals, and, of course, also characterizes those that bear more or less dark pigment. Accordingly, the diverse color patterns observed on these species (figs. 1–9) result from the addition of varying amounts of melanin to the original yellow in the cuticula.

Mechanics of the color patterns. How these variations in the color patterns are effected is suggested when one studies adults to whose yellow spaces the initial small amounts of melanin have accrued. So it is discovered that the dark pigment enters the cuticle, presumably late in the pupal stage, at certain fixed points of the body, not in a random manner. These points of entrance appear to be located chiefly in certain infolds of the cuticle, or at other places where the chitin is relatively more permeable than the intervening sclerites.

Specifically, these points of entrance appear to be as follows: the ocellar triangle and possibly the upper end of the antennal scrobe; the cervix or neck; the infolded or overlapping conjunctiva that joins the pronotum to the mesonotum; the parapsidal furrows and perhaps the alar sclerites at the bases of the wings; and the transverse infold which unites the metanotum and the propodeum.

How the diverse amounts of black invade the original yellow in these species is best illustrated by reference to the males of *M. nigrovariegatus*, because of the extreme variation in percent of dark color in this sex. In the almost wholly yellow males (fig. 1), the black on the head is confined to the limits of the ocellar triangle, whereas in the dark extreme the black matter from the triangle spreads in various directions and is also confluent with that arising from the



In these figures, the light areas represent various shades of yellow; dark areas signify brown to black spaces.

FIGS. 1–7.—Dorsal view of head, thorax and propodeum of *Megastigmus nigrovariegatus*, males. Variations in color pattern.

FIG. 8.—Same, but of *Megastigmus aculeatus*, females. Light color form from *Rosa eglanteria*, West Lafayette, Coshocton County, Ohio.

FIG. 9.—Same as 8. Dark color form from *Rosa eglanteria*, Kickapoo Park, and *R. virginiana*, Fox Ridge Park, Illinois.

neck to spread over the occiput to the compound eyes (fig. 7). The last yellow space persisting on the darkest males is a small patch on the vertex adjacent to the inner edge of each compound eye (fig. 7).

On the small light-colored males, the pronotum is entirely light orange-yellow. Melanin first appears at the middle of the front margin (fig. 4), seeming thus to issue from the cervical entrance, thence spreads laterad along the front edge. In the still darker males, it proceeds backward to varying distances and may invade the entire anterior half, commonly leaving the posterior half the original orange-yellow. In this latter condition, the yellow patches take the form of two squares (figs. 5, 6) separated by a longitudinal mesal line of black and bordered outwardly with black. In still darker males, the melanin spreads caudad to occupy more and more of these yellow squares (fig. 7), until the pronotum is entirely black, which condition obtains only in a small percent of large individuals.

The black coloring matter that enters the pronotal-mesonotal conjunctiva spreads in a similar manner to that in the pronotum. It appears not to diffuse forward into the pronotum, but only caudad into the prescutum (figs. 3, 4) and, by confluence with the melanin from the other mesonotal sutures, comes step by step to involve the entire mesonotum in case of wholly black individuals (figs. 6, 7). The metanotum retains traces of yellow in its mesial third in all but the darkest males (figs. 6, 7). The melanin that darkens the propodeum first appears along its anterior margin (figs. 2, 3), whence, in successively darker variations, it blackens the entire segment. This is one of the first areas to become wholly black.

Percental distribution of melanin. To illustrate this distribution, I choose the data pertinent to the females of *M. aculeatus*, for the reason that (a) the males are few and (b) the range of variation in color pattern is more limited and therefore more readily described than that of the males and females of *nigrovariegatus*.

As stated above, my series of 1,045 female *aculeatus* forms two distinct groups with reference to the amounts of black on the body. The lighter lot (fig. 8), reared from hips that originated in states east of Indiana, show 11 to 17 percent of black. This is distributed over the body as follows: vertex, 0 to 3 percent; pronotum, none; mesonotum, including 3 percent on each axilla, 8 to 11; metanotum and propodeum combined, 2 to 4 percent. On the other hand, the 32 to 54 percent of black on the darker group (fig. 9), obtained from Illinois parks, are distributed as follows: vertex, 4 to 11, but most individuals have 6 to 8 percent; pronotum mostly none, rarely 1 or 2 percent; mesonotum, including 3 percent on the axillae, 10 to 20 percent, but most have 13 to 18 percent; metanotum and propodeum combined, 13 to 18, but the majority with 16 percent. It was observed also that the metaepisterna of both lighter and darker lots were predominantly dark, whereas the metaepimera remained wholly pale whitish-yellow in all individuals.

CAUSES OF VARIATION IN SIZE

Disregarding, for present purposes, the possibility that genetic influences may help to regulate size in *M. nigrovariegatus* and *aculeatus*, what ecological factors may be operative to this end? First, latitude of occurrence of rose hosts and chalcids may be discarded as a possible factor, particularly in *nigrovariegatus*, for the reason that both some of the largest and smallest series of my sample originated in the northern sector of the sampled area, i.e., the vicinity of 50 degrees north latitude. For example, the highest percent of large males obtained, namely 27.65, was reared from a rose growing at Eaglesnest in northeastern Minnesota, whereas no "large" males (table 1) issued from another species sampled at Eaglesnest, and at Saskatoon and Ottawa, Canada, and Solon Springs in northwestern Wisconsin.

Yet the tabulated data indicate there is some relationship between roses and sizes of the *Megastigmi*. For example, the data (table 1) show that the higher percent of large *nigrovariegatus* developed in the hips of *Rosa acicularis*, *arkansana*, and *rugosa*, whereas the majority of the small- and medium-sized individuals originated in hips of *virginiana* and *palustris*. Observations made in 1943–1953 on the size of achenes seem to identify the particular factor in the hip with which the size of the chalcids is associated. It was there noted that the achenes of any one species of *Rosa* tend to fall within fairly definite limits as to size. Those of *R. acicularis*, *arkansana*, and *rugosa* rate as comparatively large; those of *virginiana* and *palustris* as small; whereas the achenes of *blanda* and *carolina* are generally intermediate to the above "small" and "large" ones. In other words, the size of the adult rose seed chalcids appears to be correlated with the volume of the achene.

How this correlation is implemented seems logically to involve the seed in the achene, for no characteristics of the rose hip can be so potent and direct as those which impinge on the larval insect—the stage that feeds, grows, and determines the size of the resulting adult. Growth depends wholly on the nutrients the larva can acquire from its environment. Moreover, since the seed present in a single achene is the only substance available to an individual larva, the volume and quality of the seed directly determine the size of the feeding-growing larva and consequently of the resulting adult. However, whereas the seed-food available to the larva is identified as the factor directly affecting the size of both larva and adult, volume of the seed in itself and alone appears not to account for all the

variations in size. Some exceptions to this general rule of coincidence in size of achenes of specific roses and chalcids do occur. That is, some smaller individuals may be obtained from species whose achenes generally rate as large, and vice versa.

I offer two explanations for these departures from the rule. One is that the achenes found within a particular hip, or a species of rose, may vary somewhat in size, probably due to changes in rainfall and temperatures in the course of the growing season of the hips. Second, the size of the larva is doubtlessly affected by the varying degrees or extents of concurrence between (a) the phase of larval development and (b) the condition of immaturity or maturity of the seed available to the growing larva. If, for example, the seed embryo is pulpy in texture, hence ingestible during the entire developmental life of the larva, the latter will realize its full potential of size providing the volume of the seed suffices. If, on the other hand, the seed is older by several days when feeding begins, it may turn hard and uningestible before the larva attains the full-fed state and maximum potential size, with the result that some of the subnormal larvae may nevertheless eventuate as adults, but of reduced size.

In support of my evidence, I cite the observations by Milliron (1949, p. 385) who states that the female *nigrovariegatus* ordinarily oviposits in soft seeds whose cotyledons are small and enveloped in a watery or jelly-like medium, but as the season progresses, somewhat older fruits must be selected. I consider it probable that eggs laid in such older achenes develop into smaller adults, for reasons advanced above.

From the above considerations emerges the essential idea that the wide range of size in *M. nigrovariegatus* is a reflection of the small to large seeds present in the long list of specific rose hosts in which the larva of this chalcid is known to develop. By contrast, the comparatively uniform size shown by adult *M. aculeatus* correlates with the narrow variation in size of the achenes contained in the hips of *Rosa eglanteria* and *virginiana*, from which my series was reared.

CAUSE OF VARIATION IN COLOR

The only clue afforded by my studies as to the identity of this cause is contained in the observation that variation in the color pattern, i.e., the proportional amounts of yellow and dark pigments in the cuticle, generally parallels the variation in size. The smaller and lighter-colored individuals developed in small seeds, and the larger and darker ones issued from larger seeds. In other words, small size and light color are associated in one extreme, whereas large size and larger per cents of dark pigment concur in the other. The fact that size is generally proportional to the amount or quality of the seed available to the growing larva therefore suggests that color patterns are in some way tied in with the food factor.

This generalization is supported by data for *M. nigrovariegatus* in table 1. The largest numbers of males, having high per cents of dark area, originated in the achenes of *Rosa acicularis* from northwestern Minnesota. None of the males from this source fall into the group characterized by 1 to 25 percent of black; 29.49 percent are 26 to 50 parts black, and 70.51 percent of the individuals are 50 to 100 parts black. Ranking second with reference to the extent of dark spaces on the males is the sample from *R. rugosa*, and third, the lot reared from the Alaskan *acicularis*. The point made here is that the achenes of these *Rosa* spp. are the largest met with in this project, and that they yielded not only the largest but simultaneously also the darkest males.

Moreover, the principle that large size and dark color coincide generally with large achenes is exemplified, although negatively, by the observation that the smallest, lightest males developed in the achenes of *R. palustris* and *carolina*, which are the smallest achenes found. Intermediate to the above extremely dark and light males are those reared from the hips of *R. blanda* and the mixtures of *blanda* and *carolina* that grew intermingled along a railroad at Chetek, Wisconsin.

Although the females of *nigrovariegatus* show a lesser degree of variation in color than the males, the existing variation conforms to the same principle observed in the males, that the darker fraction of females is at the same time the largest in size, and develops in hips containing the larger achenes, whereas the predominantly yellow and smaller fraction issued from rose species that produce smaller achenes.

These instances point to the probability that variation in color pattern, like variation in size, is an expression of the food factor in the larva, and that the cause of variation in both size and color is basically physiological-nutritional.

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EIGHT NEW CHIGGERS FROM EAST AFRICA AND A NEW GENUS, TROMBIGASTIA (ACARINA: TROMBICULIDAE)[1]

P. H. VERCAMMEN-GRANDJEAN AND JAMES M. BRENNAN[2]

INTRODUCTION

The new species included in this study are from collections in the Rocky Mountain Laboratory and the Chicago Natural History Museum as recorded below:

	RML Accession Number	Number of Specimens	Specimen Number	Collectors
Rocky Mountain Laboratory:				
I *Trombicula ugandae* n. sp.	31124	1	11652/P/1	Haddow, A. J. and Lumsden, W. H. R.
II *Trombicula rossi* n. sp.	31469	5	26452/P/1–5	Ross, R. W.
III *Trombicula mini* n. sp.	31305	7	30552/P/1–7	"
IV *Schöngastia hyracis* n. sp.	31469	5	26452/S/1–5	"
"	31305	2	30552/S/1–2	"
"	31121	16	0552/S/1–16	"
V *Euschöngastia striata* n. sp.	31121	4	0552/R/1–4	"
VI *Acomatacarus mutabilis* n. sp.	31305	1	30552/A/1	"
Chicago Natural History Museum:				
VII *Trombigastia cadei* n. g., n. sp.	32048	10	11950/T/1–10	Cade, C. E.
VIII *Whartonia oweni* n. sp.	31773	11	30850/W/1–11	Owen, J.
"	31776	10	4456/W/1–10	"

Holotypes are No. 1 of their respective series and are deposited as follows: II, III, IV, and V in the Royal Museum of the Belgian Congo, Tervuren, Belgium; I and VI in the collection of Vercammen-Grandjean; VII and VIII in the Chicago Natural History Museum, U.S.A.

The first three belong to a group which one of us (P.H. V.-G.) is describing soon as a new genus, near *Trombicula*, in the light of a character hitherto unapplied.

Schöngastia hyracis is a clear-cut representative of its genus.

Euschöngastia striata will be treated shortly as a member of a new subgenus of *Euschöngastia*.

Trombigastia cadei is the basis for a new genus described below.

Acomatacarus mutabilis is described from a single specimen, obviously a freak, since it has only one (eccentric) AM.

The last one, *Whartonia oweni*, a large species, is the first of its genus reported from Africa.

[1]The coauthors collaborated fully in the preparation of this paper, originally written in French by the senior author, then translated into English and revised by the junior author. Accepted for publication Feb. 4, 1957.

[2]From the Provinicial Medical Laboratory of Kivu, Bukavu, Belgian Congo, and the U. S. Department of Health, Education, and Welfare, Public Health Service, National Institutes of Health, National Institute of Allergy and Infectious Diseases, Rocky Mountain Laboratory, Hamilton, Montana, respectively.

ABBREVIATIONS AND USAGE

The greater part of the abbreviations used in this paper are well-known. Others are: ga = anterior genuala, gp = posterior genuala, tp = posterior tibiala, MTp = posterior mastitarsala, gm = median genuala, μgm = median microgenuala, pa, pm, and pp = lengths of anterior, median, and posterior legs respectively, Ip = leg index, the sum of the lengths of the legs. Ip is relatively constant and a more precise measurement than body length and width. From it the real size of a trombiculid larva can be interpreted (Vercammen-Grandjean *et al.*, in manuscript).

Bars or internal annular thickenings of the leg segments = b, semi-bars or semi-annular thickenings = sb.

The palpal formula, derived from the structure and vestiture of the palp, is expressed with the following abbreviations: B = branched seta, P = plumose seta, N = nude seta, E = striated spur, G = tibial claw (number of prongs being indicated), ( ) = dorsal position, — = separation of segments.

Trombicula ugandae n. sp.

(Fig. 1—A, B, F; Fig. 2—A, B, E)

Measurements: AW–58, PW–68, SB–20, ASB–25, PSB–29, SD–54, AP–23, AM–34, AL–26, PL–40, S—, H–38, D–34/27, V–22/27, pa–250, pm–210, pp–242, Ip–702. For comparison, the following measurements are given of *Neotrombicula saperoi* Radford 1954: AW–65, PW–80, SB–20, ASB–30, PSB–30, SD–60, AP–30, AM–33, AL–34, PL–40, S–70, H—, D–40, V—, ap—, mp—, pp—, Ip—.

Dorsum: Scutum pentagonal, with antero-

lateral shoulders and AL behind level of AM. PL>AM>AL. Scutal setae densely barbed, similar to dorsal and postanal setae. Puncta fine and numerous, much different than the scattered puncta of *N. saperoi*. Eyes in two pairs, posterior one degenerate. Setal formula: 2–10–8–8–4–4–2=38; for *saperoi*, 2–8–8–6–6–4–4–2=40.

Venter: Anus between fourth and fifth rows of ventral setae. The two pairs of sternal setae are plumose. Setal formula is 6–6–6–4–6–2–2=32; total for *saperoi* is 58.

Legs: Segments 7–7–7. Coxae punctate, not striate. Principal smooth setae: 2 ga, 1 gp, 1 tp, 1 MTp in median position. Tarsal bars: b.2sb–b–b.sb. Coxal and sternal setae are plumose and differ greatly from those of *T. rossi*.

Gnathosoma: Gnathobase punctate. Galeal seta nude. Chelicera with usual tricuspid cap. Palpal formula:
(P)–(B)–(B).N.B.G_3–E.B.B.B.B.(B).(P).

Type data: Described from a single larval specimen, the holotype, taken from eyelid of a dog (*Canis familiaris*), Entebbe, Uganda, 11 June 1952.

Trombicula rossi n. sp.

(Fig. 1—C, E, F; Fig. 2—C, D, E)

Diagnosis: Scutum roughly pentagonal with anterolateral shoulders, and AL behind level of AM. Palpal claw trifurcate. Galeal seta nude. Three genualae I, a genuala III, a tibiala III, and a mastitarsala III near the base. Chelicerae spurred.

Measurements: Average of 5 specimens: AW–75, PW–91, SB–32, ASB–28, PSB–36, SD–64, AP–28, AM–31, AL–29, PL–38, S–64, H–41, D–36/29, V–27/29, pa–261, pm–223, pp–258, Ip–742.

Dorsum: Scutal setae densely barbed. PL>AM>AL. Scutal puncta fine and numerous. Filiform sensillae with 8 to 10 branches. Eyes 2/2; the posterior ones degenerate. Setal formula: 2–8–8–6–6–4–2=36.

Venter: Anterior sternal setae with 2 to 4 long branches, posterior sternal setae appearing nude but actually with 2 to 4 barely visible, fine, appressed barbules. Anus between fourth and fifth rows of ventral setae. Setal formula: 6–6–6–4–4–6–2=34.

Legs: Segments 7–7–7. Coxae punctate. Principal smooth setae: 3 ga, 1 gp, 1 tp, 1 MTp near the bar. Tarsal bars: b.2sb–b–b.sb. Coxal setae, like the posterior sternals, with 2 to 4 branches, the medians with 2 to 5 barely visible, fine appressed barbules. Ip very large in comparison to that of *T. mini* (742 as against 618).

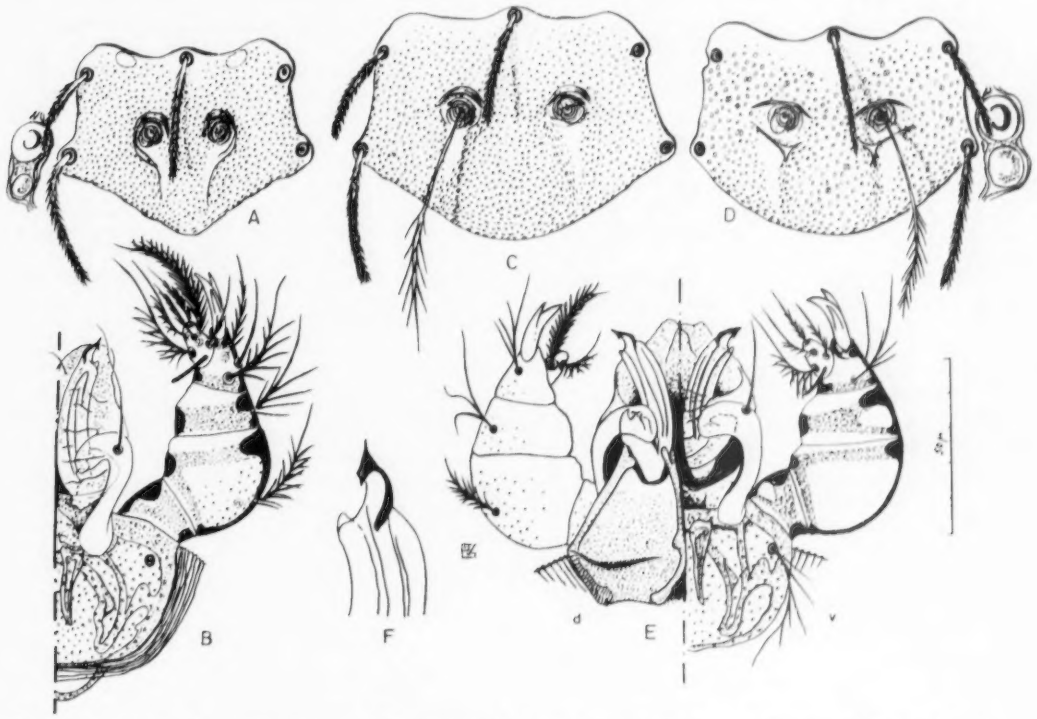

FIG. 1. A. scutum, B. gnathosoma, and F. cheliceral blade of *T. ugandae* n. sp.; C. scutum, E. gnathosoma, and F. cheliceral blade of *T. rossi* n. sp.; D. scutum, E. gnathosoma, and F. cheliceral blade of *T. mini* n. sp.

Gnathosoma: Gnathobase punctate. Galeal setae nude. Chelicerae crowned with a tricuspid cap and spurred. Palpal formula: (P)–(B)–(B).N′.B.G$_3$–E.B.B.B.B.(B).(P). (N′ = sometimes nude, sometimes provided with a fine barb).

Type data: Holotype (larva) and 4 paratypes (larvae) from *Hyrax* sp., Kaabong, Uganda, 26 April 1952.

Named for the collector, Dr. R. W. Ross.

Trombicula mini n. sp.

(Fig. 1—D, E, F; Fig. 2—C, D, E)

Diagnosis: Similar to *T. rossi*.

Measurements: Average of 5 specimens: AW–68, PW–78, SB–28, ASB–26, PSB–34, SD–60, AP–28, AM–33, AL–29, PL–41, S–60, H–40, D–34/29, V–24/29, pa–216, pm–184, pp–218, Ip–618.

Dorsum: Scutum smaller and the posterior angle less acute than in *T. rossi*. Puncta larger, more irregular, and more sparsely distributed. Sensillae with 16 to 22 branches. Other characters as in *T. rossi*.

Venter: As in *T. rossi*.

Legs: As in *T. rossi*, but shorter.

Gnathosoma: Morphologically the same as that of *T. rossi*, but with dimensions more reduced.

Type data: Holotype (larva) and 6 paratypes (larvae) from *Hyrax* sp., Kaabong, Uganda, 30 May 1952.

Schöngastia hyracis n. sp.

(Fig. 3)

Measurements: Average of 12 specimens: AW–57, PW–83, SB–17, ASB–29, PSB–29, SD–52, AP–31, AM–31, AL–67, PL–55, S–29, H–46, D–42/38, V–32/38, pa–301, pm–247, pp–298, Ip–846.

Dorsum: Eyes 2/2, the anterior large, the posterior small and degenerate. Scutum subpentagonal. Puncta normal and numerous. Sensillary bases close together and in line with PL. Sensillae globose, armed with large but poorly defined setules. AL>PL>AM. Scutal setae with numerous and long barbs, especially AL and PL. AM, the other dorsal setae, and postanal setae have shorter but equally numerous barbs. Setal formula: 2–8–6–6–4–4–2–2=34.

Venter: Sternal setae plumose. Anus between fourth and fifth rows of setae. Setal formula: 6–4–4–4–6–4–2=30.

Legs: Segments 7–7–7. Coxae punctate. Principal smooth setae: 3 ga, 1 gp, 1 tp, 1 MTp on basal third of tarsus. Tarsal bars: b–b–b. Coxal setae plumose. The large Ip (846) suggests a species somewhat larger than average.

Gnathosoma: Gnathobase punctate. Galeal seta nude. Chelicerae armed with the usual tricuspid cap and 5 to 8 dorsal teeth. Palpal formula: (B′)–(N)–(N).N.N.G$_3$–E.B.B.B.N.B.(B).(B).(P). (B′) = femoral seta branched, but having only 2 to 4 short and fine branches.

Type data: Holotype (larva) and 4 paratypes (larvae) from *Hyrax* sp., Kaabong, Uganda, 26 April 1952; 2 paratypes, same host and locality, 30 May 1952; 16 paratypes from "lizard or hyrax?" (probably the latter), Karamoja, Uganda, May 1952.

Euschöngastia striata n. sp.

(Fig. 4)

Measurements: Average of 3 specimens: AW–60, PW–80, SB–23, ASB–27, PSB–24, SD–51, AP–26, AM–29, AL–26, PL–36, S–38, H–33, D–30/28, V–21/28, pa–226, pm–190, pp–210, Ip–626.

Dorsum: Scutum large and subpentagonal, punctate and partially striate, provided with stiff setae having short barbs arranged like a head of grain. AM behind level of AL. PL>AM>AL. Fusiform sensillae with long setules. SB at level of PL. Scutal puncta relatively scattered. Two pairs of eyes, the anterior larger. Dorsal setae similar to scutal and postanal setae. Setal formula: 2–8–6–6–4–4=30.

Venter: Two pairs of plumose sternal setae. Anus between third and fourth rows of setae. Setal formula: 6–4–4–4–2=20.

Legs: Segments 7–7–7. Coxae punctate and striate. Principal smooth setae: 3 ga, 1 gp, 1 tp, 1 MTp toward middle of tarsus. Tarsal bars b–b–b. Coxal setae plumose. Ip small, thus a small species.

Gnathosoma: Gnathobase punctate and striate. Galeal setae nude. Chelicerae with tricuspid cap and spurred. Palpal formula: (N)–(N)–(N).N.N.G$_3$–E.B.B.B.N.B.(B).(B).(P).

Type data: Holotype (larva) and 3 paratypes (larvae) from "lizard or hyrax ?", Northeast Karamoja, Uganda, May 1952.

Although confusion in labelling is apparent, *E. striata* is thought to be a parasite of reptiles.

Trombigastia n. g.

(Fig. 7)

The creation of this new genus aims to classify certain larval Trombiculinae, all parasitic on bats, for which it is impossible to find an adequate place in the present system. These parasites are, in effect, neither altogether like *Trombicula* nor completely like *Schöngastia*. Their sensillae are often on the border line between filiform and claviform which, by definition, designates the one or the other of these two groups of Trombiculinae. For this reason we give the hybrid generic name *Trombigastia*. The position of the new genus is near *Euschöngastia*, not far from *Schouteden ichia*, and linked to *Trombicula sens. lat.* Although *Schöngastia lipoxena* Womersley has obvious claviform sensillae, we think it may properly be referred to *Trombigastia*.

Genotype, **Trombigastia cadei** n. sp.

Description: Scutum trapezoidal with sinuous anterior border and concave lateral and posterior borders, very similar to the scutum of *Schoutedenichia*. Sensillae slightly swollen and furnished with long barbules. Level of SB well in front of PL. Spurs of anterior tarsi and of palpal tarsi very long. Two bars on anterior tarsi. Palpal tarsi always with 7 more or less barbed setae, no nude subterminala. Three anterior genualae. Posterior legs with long and thin genuala and tibiala; their tarsi bearing a long and strong seta, lightly barbed, in the usual position of a mastitarsala. On Plate 7 we have figured (D) the chelicera representative of *Trombigastia*, and (E) the stubby and specialized chelicera of *S. lipoxena* which, nonetheless, is fundamentally like the other species we are placing in the genus. At present we include the following 6 species:

Trombicula harrisoni Womersley, 1952, from *Hipposideros* sp., Kepong, Malaya; *T. dimolinae* Audy, 1952, from *Rhinolophus* sp., Kepong, Malaya; *T. brevitarsa* Radford, 1954, from *Rhinolophus clivosus acrotis*, Ta'izz, Yemen; *T. mounti* Radford, 1954, from *Nycteris capensis damarensis*, Asmara, Eritrea; *Schöngastia lipoxena* Womersley, 1952, from *Hipposideros* sp., Kepong, Malaya; *Trombigastia cadei* n. sp. from *Miniopterus* sp., Ngong, Kenya.

Trombigastia cadei n. sp.

(Figs. 5 and 6)

Measurements: Average of 6 specimens compared to those of the other species (average measurements based on those given by the respective authors):

	AW	PW	SB	ASB	PSB	SD	AP	AM	AL	PL	S	H	D	V	pa	pm	pp	Ip
harrisoni:	48	62	20	30	14	44	38	41	42	48	69	46	40/28	25/28	260	234	260	754
lipoxena:	45	60	21	21	14	35	27	36	32	47	62	35	53/30	34/27	220	195	220	635
dimolinae:	45	64	18	25	16	41	34	47	36	57	68	45	42/32	27/32	230	185	210	625
brevitarsa:	70	90	20	30	20	50	40	50	50	56	62	—	45	—	—	—	—	—
mounti:	47	69	18	27	18	45	37	42	34	45	66	44	39/33	25/33	262	223	247	732
cadei:	60	77	23	30	21	51	42	49	49	64	58	64	58/36	31/36	271	233	281	785

N.B. The greatest diameter of the senilla of *T. mounti* is 1.6 μ.

Dorsum: Scutum trapezoidal, anterior margin bi-concave, lateral and posterior margins concave; punctate; setae finely and densely barbed; sensillae somewhat thickened, finely barbed. PL > AM = AL. Level of SB in front of PL. Two pairs of ocelli, the anterior larger. Dorsal setae like the scutal and postanal setae. Setal formula: 2–8–6–6–8–8–6–2 = 46.

Venter: Two pairs of plumose sternal setae. Anus between fourth and fifth rows of setae. Setal formula: 4–6–4–4–4–4–4–6–4–2 = 42.

Legs: Segments 7–7–7. Coxae punctate. Spur of anterior tarsus very long (compare the tarsal spurs of *T. mounti* (Tm), *T. harrisoni*, (Th) and *T. lipoxena* (Tl) in Plate 7,A). Principal smooth setae: 3 ga, 1 gp and 1 tp, long, MTp with 2 to 3 fine basal barbs. Tarsal bars 2b–b.sb–b.sb. Dorsal setae of legs generally with only 2 to 3 branches. Ip large, indicating the largest species in the genus.

Gnathosoma: Gnathobase punctate. Galeal setae bare. Chelicerae armed with a tricuspid cap of three pointed processes, one dorsal and two lateral, and a latero-external spur. Palpal formula:
(P)–(B)–(B).B.B.G_3–E.B.B.B.B.B.(B).(P).
The tibial claw is very long and the prongs are short. The tarsal spur is very long.

Type data: Holotype (larva) and 9 paratypes (larvae) from *Miniopterus* sp., Ngong, southern Kenya, 11 September 1950.

Named for the collector, C. E. Cade.

Acomatacarus (Acomatacarus) mutabilis n. sp.

(Fig. 8)

Measurements: Holotype: AW–67, PW–88, SB–29, ASB–34, PSB–19, SD–53, AP–28, AM–42, AL–47, PL–64, S–79, H–62, D–58/33, V–20/35, pa–245, pm–204, pp–266, Ip–715. For comparison, measurements of *A. arabicus* Radford, 1954, which *A. mutabilis* resembles, are given: AW–63, PW–82, SB–32, ASB–30, PSB–20, SD–50, AP–22, AM–22, AL–34, PL–40, S–62, H—, D–30, V—, pa—, pm—, pp—, Ip—.

Dorsum: Scutum large, with rounded margins; puncta large and scattered but not encroaching on certain areas. Scutal setae moderately and finely barbed. A single, eccentric AM (an anomalous condition). PL > AL > AM. Sensillae filiform, distally with 4 to 6 fine and short barbs. SB at level of PL. Eyes 2/2, contiguous, the anterior larger. Six humeral setae between median and posterior coxae; these should be counted with the dorsal humerals. Setal formula: 8–10–10–4–8–8–8–6–6–4–4 = 76.

Venter: One pair of plumose sternal setae. Spiracles between gnathobase and anterior coxae, tracheae not visible. Anus between fourth and fifth rows of setae. Setal formula: 10–10–12–8–4–10–6 = 60.

Legs: Segments 6–6–6. Coxae punctate. Coxal setal formula: 2P–P–P. Tarsal bars: 2b–2b–2b. Principal smooth setae: 2 ga, 1 gm + 1 μgm, 1 gp, 1 tp; 2 mastitibialae and 2 mastitarsalae, both structures with minute basal barbs.

Gnathosoma: Gnathobase punctate. Galeal

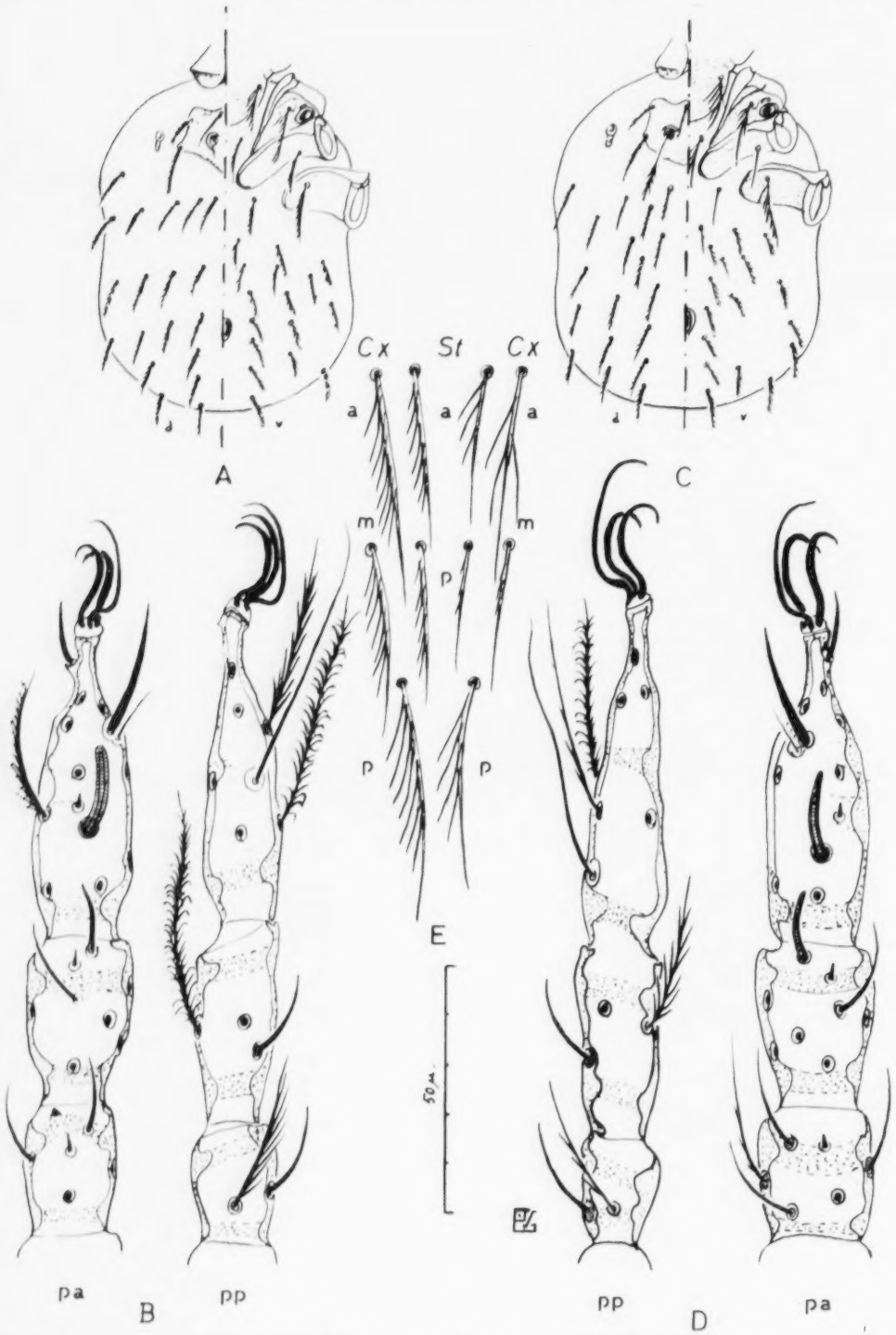

FIG. 2. A, dorsum and venter, B, anterior and posterior legs, and E, (left side) coxal (Cx) and sternal (St) setae of *T. ugandae* n. sp.; C, dorsum and venter, D, posterior and anterior legs, and E, (right side) coxal and sternal setae of *T. rossi* n. sp.

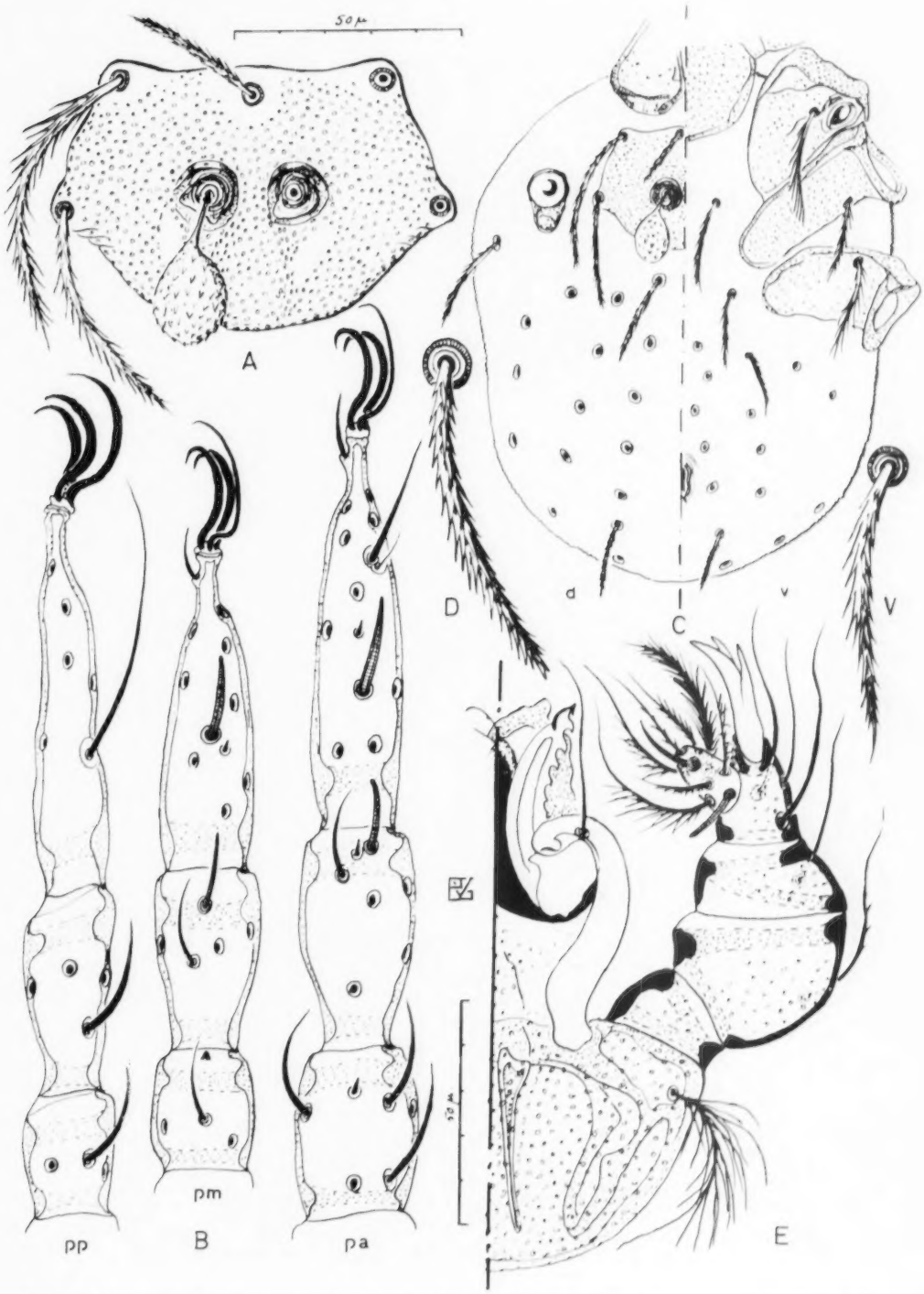

FIG. 3. *Schongastia hyracis* n. sp. A, scutum, B, posterior, median, and anterior legs, C, dorsum and venter, D, a dorsal seta, E, gnathosoma, V, a ventral seta.

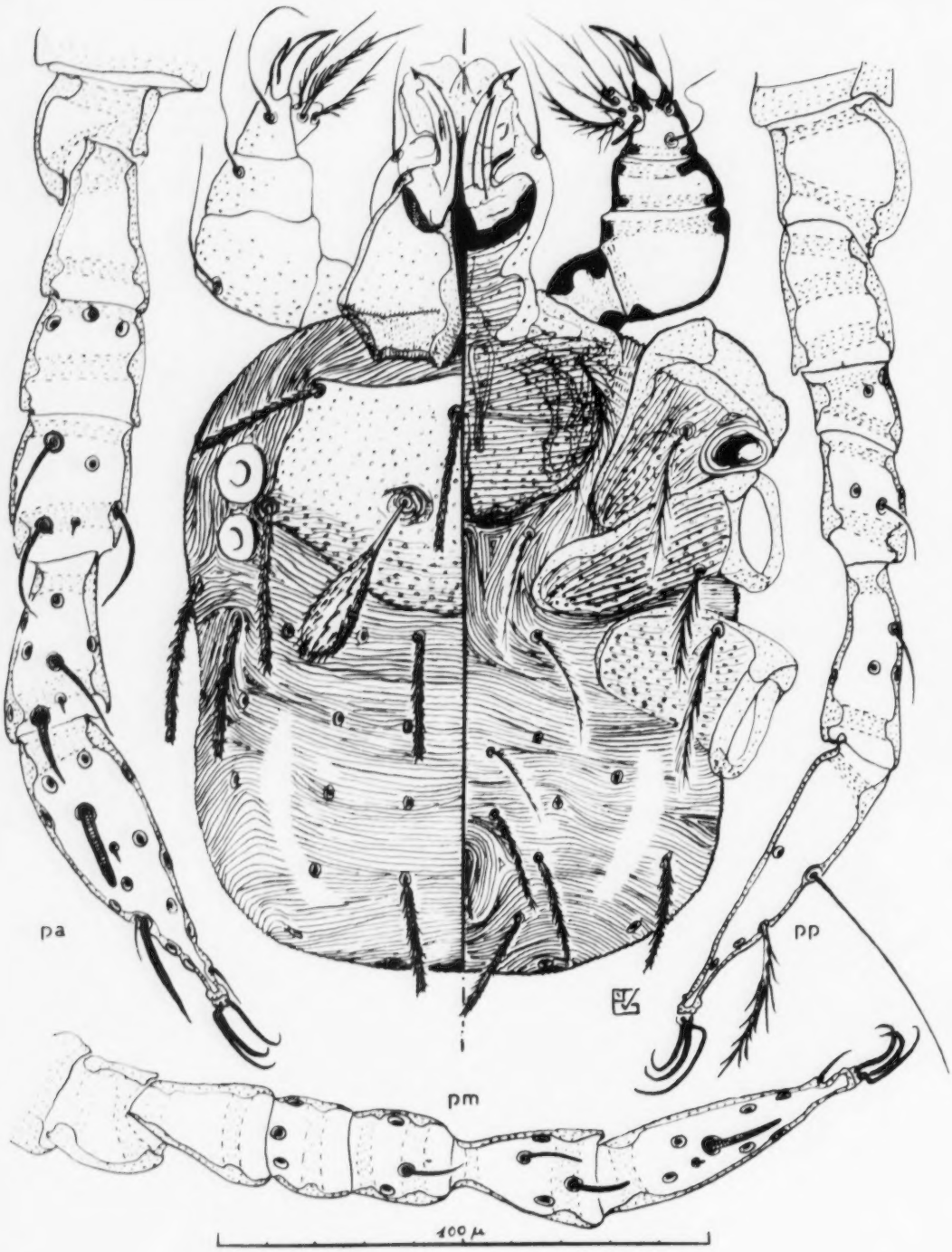

FIG. 4. *Euschöngastia striata* n. sp.

Fig. 5. *Trombigastia cadei* n. g., n. sp.

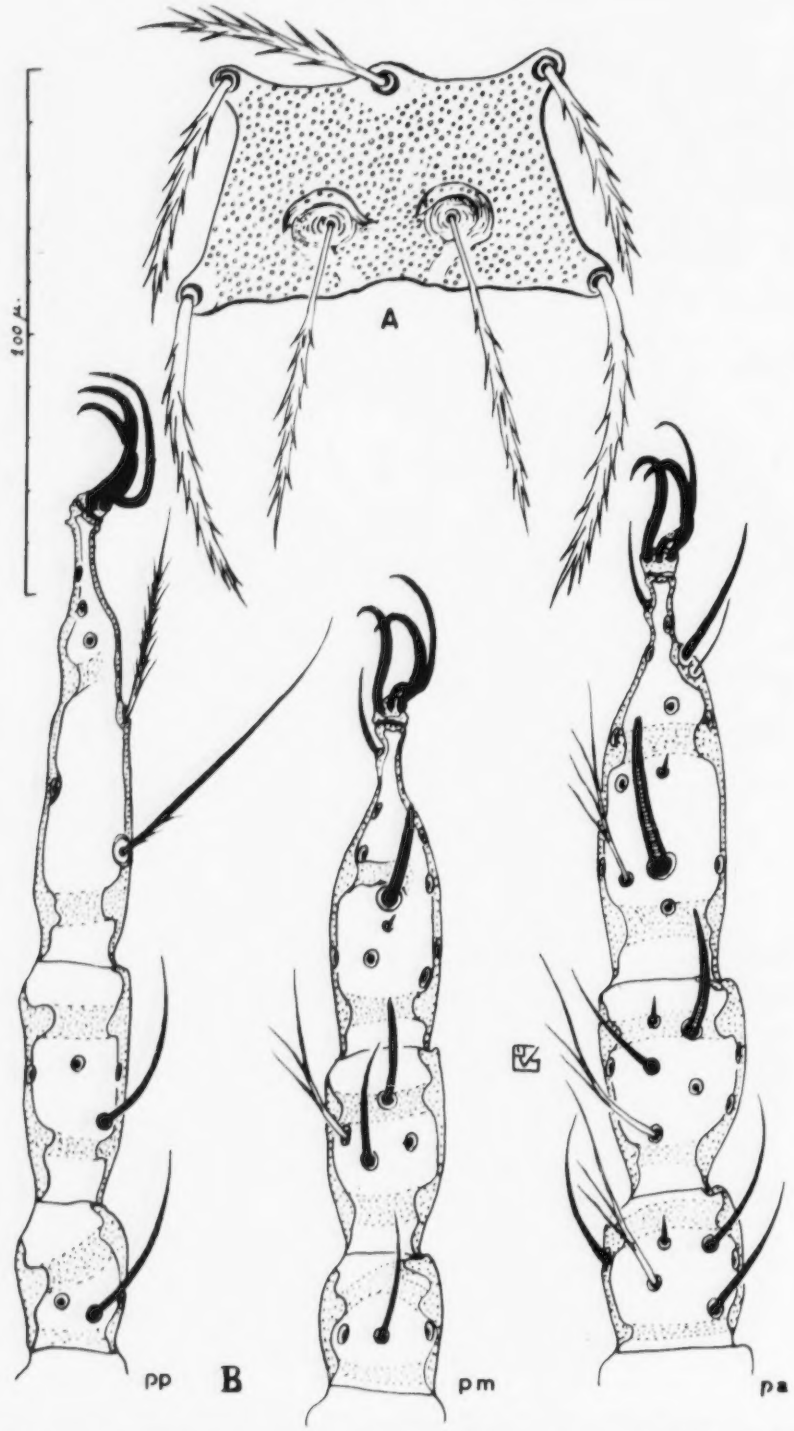

FIG. 6. *Trombigastia cadei* n. g., n. sp. A. scutum, B, posterior, median, and anterior legs.

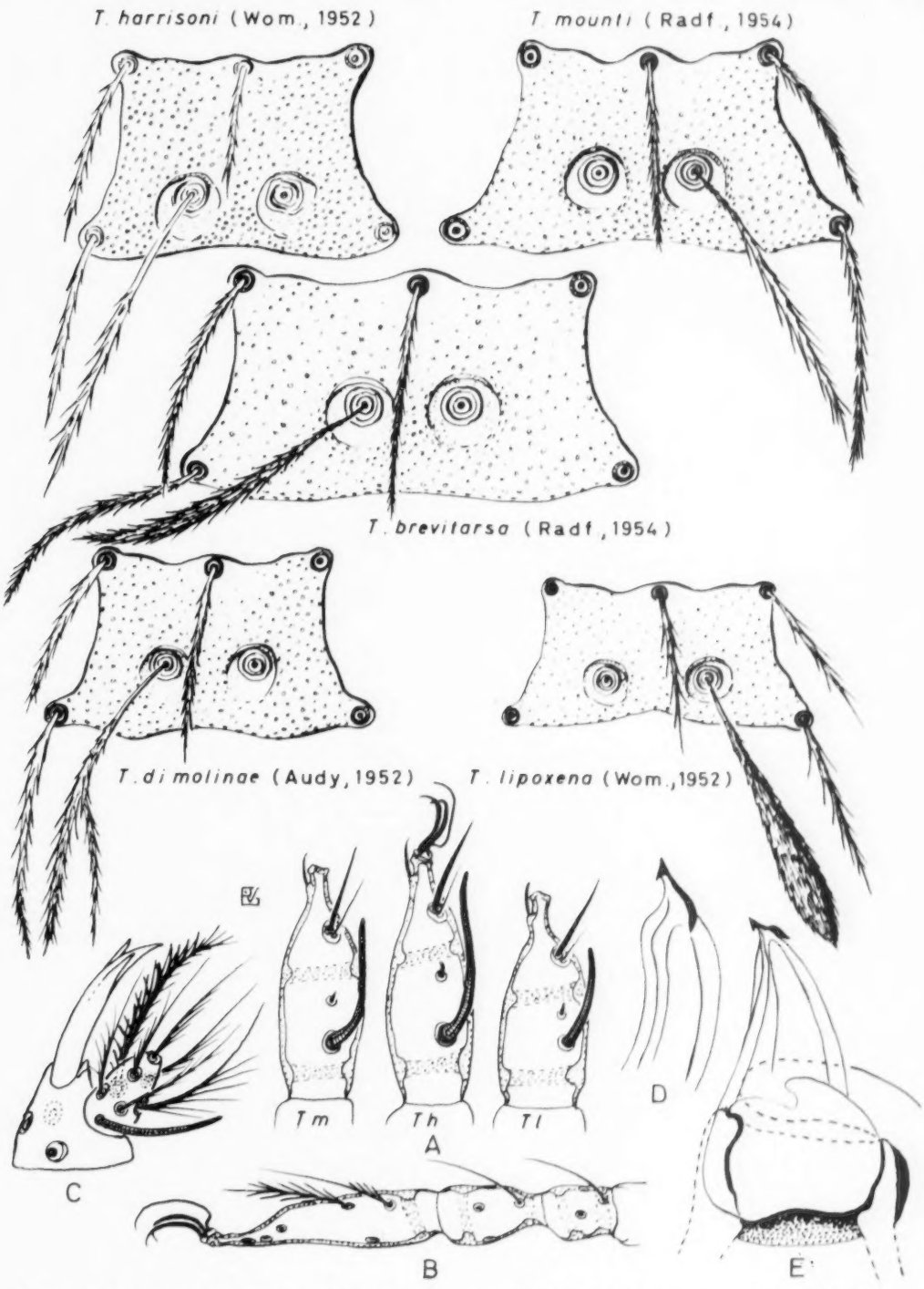

FIG. 7. *Trombigastia* n. g. Scutums of 5 species; A. anterior tarsus of *T. mounti* (Tm), *T. harrisoni* (Th), and *T. lipoxena* (Tl); B. posterior leg of *Trombigastia* spp. showing basally barbed mastitarsala; C. tibia and tarsus of palp of *Trombigastia* spp.; D. cheliceral blade of *Trombigastia* spp.; E. cheliceral blade of *T. lipoxena*.

FIG. 8. *Acomatacarus mutabilis* n. sp. A. scutum, B. dorsum and venter, C. palpal tibia and tarsus, D. anterior, median, and posterior legs, E. lateral and dorsolateral surfaces of cheliceral blade.

FIG. 9. *Whartonia oweni* n. sp. A. scutum, B. dorsum and venter, C. anterior, median, and posterior legs, D. dorsolateral surface of cheliceral blades, E. lateral surface of cheliceral blade, galea and galeal seta.

setae finely barbed. Chelicerae armed with a tricuspid cap and a series of ventral teeth directed externo-laterally (E,p = profile, f = face). Palpal formula:
(P)–(B)–(P).B.B.G_3–E.B.B.B.B.(B).-(B).(P).

Type data: Described from a single, aberrant larval specimen, the holotype, from *Hyrax* sp., Kaabong, Uganda, 30 May 1952.

Whartonia oweni n. sp.
(Fig. 9)

The description of this species constitutes the first record of *Whartonia* in Africa. Only 5 other species are included in the genus, 3 from North America, 1 from Islands of the Pacific (Wharton and Fuller, 1952), and 1 from India (Hiregaudar and Bal, 1956).

Measurements: Average of 16 specimens, AA–19, AW–89, PW–100, SB–34, ASB–40, PSB–20, SD–60, AP–33, AM–68, AL–55, PL–78, S–112, H–75, D–72/57, V–45/57, pa–466, pm–408, pp–486, Ip–1360. (AA = distance between AM's).

Dorsum: Scutum large, finely and densely punctate, no anteromedian projection. The 6

scutal setae normally with short barbs. PL>AM>AL. Sensillae with short basal barbules, smooth distally. Two pairs of enormous eyes, the anterior somewhat larger. Six humeral setae between median and posterior coxae; these should be included with the dorsal humerals. Setal formula: 8–6–8–8–10–10–4–2=56.

Venter: Vestigial spiracular folds between gnathobase and anterior coxa. Tracheae not visible. One pair of plumose sternal setae. Anus typically between third and fourth rows of setae. Setal formula: 8–8–6–4–6–6–4–2=44.

Legs: Segments 6–6–6. Coxae punctate. Coxal setal formula: 2P–P–P. Tarsal bars: 2b–2b–2b. Three bars on all femora and tibiae. Principal setae: 2 ga, 1 gm+1 μgm, very long and strong gp and tp, 1 MTp.

Gnathosoma: Gnathobase punctate. Galeal setae with fine and short barbs basally. Chelicerae armed with especially strong teeth. Palpal formula: (P)–(B)–(P).N.B.G_3–E.B.B.B.B.(B).(B).(P).

Type data: Holotype (larva) and 10 paratypes (larvae) from *Rhinolophus eloquens*, Torit, Equatoria, Sudan, 30 August 1950; 10 paratypes from *Rousettus* sp., Imatong Mountains, Sudan.

Named for the collector, J. Owen.

SUMMARY

The larvae of 8 new East African species of Trombiculidae and a new genus, *Trombigastia*, based on 1 new and 5 older species, are described. The new species are *Trombicula ugandae* off *Canis familiaris; T. rossi, T. mini, Schöngastia hyracis,* and *Acomatacarus mutabilis* off *Hyrax* sp.; *Euschöngastia striata* presumably off lizard; *Trombigastia cadei* (genotype) off *Miniopterus* sp.; *Whartonia oweni* (first record of this genus from Africa) off *Rhinolophus eloquens* and *Rousettus* sp.

The new genus appears to occupy an intermediate position between *Trombicula*-like and *Schöngastia*-like genera in the subfamily Trombiculinae.

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THE SPECIALIZED HEAT-SENSITIVE AREAS OF THE MOROCCAN LOCUST, DOCIOSTAURUS MAROCCANUS (THUNBERG), AND OF SEVERAL CLOSELY-RELATED SPECIES[1]

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At the conclusion of a study of the specialized heat-sensitive areas on the surface of the body of more than 120 species of grasshoppers and locusts (Slifer, 1953b) it was stated that: "Those species of locusts and grasshoppers which occur in such large numbers as to be grave agricultural pests are all well provided with heat-sensitive areas." The investigation had included such important plague species as *Locusta migratoria migratorioides* (Reiche and Fairmaire), *Locustana pardalina* (Walker), *Nomadacris septemfasciata* Serville, *Schistocerca gregaria* (Forskål), *Camnula pellucida* (Scudder), *Melanoplus bivittatus* (Say), *Melanoplus differentialis differentialis* (Thomas), *Melanoplus differentialis nigricans* Cockerell, *Melanoplus femur-rubrum femur-rubrum* (DeGeer) and *Melanoplus keeleri luridus* (Dodge). Several other species which are of major economic importance had to be omitted because preserved material in suitable condition for study could not be obtained at the time. *Dociostaurus maroccanus* (Thunberg), the Moroccan locust, was one of these. Later, through the kindness of Mr. J. P. Dempster of the Department of Agriculture in Nicosia, Cyprus and Dr. S. Okay of the Department of Zoology at the University of Ankara in Ankara, Turkey, well-preserved specimens of the Moroccan locust were obtained and the results of an examination of this material are recorded here. In addition, a study has been made of four species which are closely related to the Moroccan locust. These were furnished by Dr. B. P. Uvarov of the Anti-Locust Research Centre in London.

MATERIALS AND METHODS

The specimens of the Moroccan locust which were used in this investigation had been preserved in 5% formalin. Each individual was measured and its body length, height of the mesothorax in front of the coxae and the width of the meta-

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thorax in front of the coxae recorded. From these three linear measurements the total body surface area—exclusive of the area of the appendages—was estimated with the help of a formula developed earlier (Slifer, 1954b). After the removal of the antennae, mouth parts and legs the specimen was separated into several pieces and these were warmed gently for a few minutes in a solution of potassium hydroxide. Each piece was then washed thoroughly and examined in water under a binocular dissecting microscope with a strong light so placed that the cuticle was illuminated from the side. The heat-

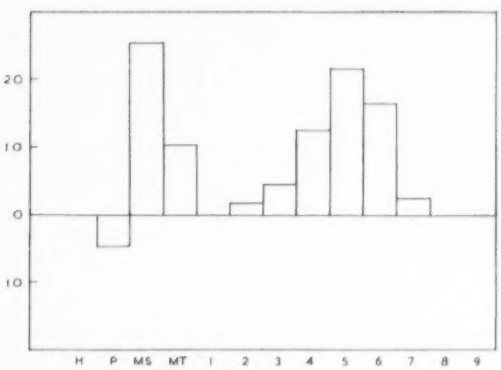

FIG. 1. Histogram showing pattern of heat-sensitive areas for a *Dociostaurus maroccanus* male. Each space on zero base-line represents a body part, H, head; P, prothorax; MS, mesothorax; MT, metathorax; 1 to 9, abdominal segments one to nine. Rectangles extending above base-line represent heat-sensitive areas on dorsal surface and those extending below it represent heat-sensitive areas on ventral surface. Percentage of total heat-sensitive area which is present on each body part indicated by height of rectangle.

sensitive areas, because of the peculiar structure of the cuticle, are silvery in appearance under these conditions and so are easily located. The parts of the body surface which contained these specialized areas were trimmed to a convenient size and flattened in water on a microscope slide under a cover glass. An outline of each heat-sensitive area was drawn with the help of a camera lucida and the area of the drawing obtained with a planimeter. After suitable calculations that percentage of the total body surface which was occupied by the heat-sensitive spots was determined.

The four species of Acrididae closely related to the Moroccan locust which were studied were *Dociostaurus brevicollis* (Eversmann), *Dociostaurus genei* (Ocskay), *Notostaurus anatolicus* (Krauss) and *Chorthippus albomarginatus* (DeGeer). These were obtained as dried, pinned museum specimens. Such material is much less satisfactory for work of the kind described here than is that which is fixed, for the heat-sensitive areas are not sharply delimited after treatment of the cuticle with alkali. For this reason only the presence or absence of the specialized areas was recorded and the spots were not drawn or measured.

Results and Discussion

The results of the examination of ten male specimens of the Moroccan locust are summarized in Table I. It will be noticed that the number of heat-sensitive spots varies from two to ten pairs and that these occupy from 0.04% to 0.37% of the total body surface. The variation found here is far greater than that which was found earlier in a similar study of twenty *Melanoplus keeleri luridus* males (Slifer, 1954a). A histogram showing the pattern of heat-sensitive spots for one of the *D. maroccanus* males is shown in figure 1. Table II shows the ten females studied to be much less variable than were the males. Here the number of pairs of specialized spots

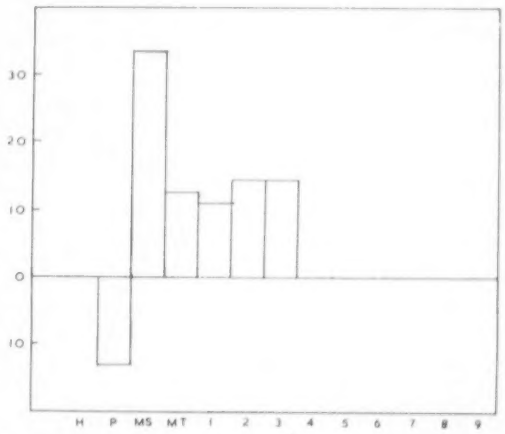

FIG. 2. Histogram showing pattern of heat-sensitive areas for a *Dociostaurus maroccanus* female. Each space on zero base-line represents a body part, H, head; P, prothorax; MS, mesothorax; MT, metathorax; 1 to 9, abdominal segments one to nine. Rectangles extending above base-line represent heat-sensitive areas on dorsal surface and those extending below it represent heat-sensitive areas on ventral surface. Percentage of total heat-sensitive area which is present on each body part indicated by height of rectangle.

ranges only from five to seven and the surface area occupied by the spots lies between 0.15 and 0.35 percent. In figure 2 a histogram is presented for the female selected as most representative of the group.

Antennal crescents were found in none of the males and the only pair of fenestrae which was present in every individual of this sex was that on the dorsal surface of the mesothorax. Only one male lacked the metathoracic fenestrae and all but one possessed fenestrae on the fifth and sixth abdominal terga. In contrast to the males, the females showed a much more regular distribution of the specialized areas. As in the males, no

TABLE I

HEAT-SENSITIVE AREAS OF TEN *Dociostaurus maroccanus* MALES. INDIVIDUALS ARRANGED IN ORDER ACCORDING TO NUMBER OF THESE SPECIAL AREAS. NUMBER OF BODY PARTS WITH SPECIAL AREAS, PERCENTAGE OF THE TOTAL BODY SURFACE OCCUPIED BY THEM AND TOTAL BODY SURFACE AREA SHOWN FOR EACH

INDIVIDUAL	NUMBER OF PAIRS OF SPOTS	NUMBER OF BODY PARTS WITH SPOTS	TOTAL BODY SURFACE	
			PERCENT OCCUPIED BY SPOTS	($mm.^2$)
1	2	2	0.07	320
2	5	5	.12	292
3	5	5	.04	295
4	5	5	.10	336
5	7	7	.13	306
6	8	8	.12	333
7	9	9	.37	255
8	9	9	.17	272
9	9	9	.13	327
10	10	10	.29	311
Means	7	7	0.15	305

TABLE II

HEAT-SENSITIVE AREAS OF TEN *Dociostaurus maroccanus* FEMALES. INDIVIDUALS ARRANGED IN ORDER ACCORDING TO NUMBER OF THESE SPECIAL AREAS. NUMBER OF BODY PARTS WITH SPECIAL AREAS, PERCENTAGE OF THE TOTAL BODY SURFACE OCCUPIED BY THEM AND TOTAL BODY SURFACE AREA SHOWN FOR EACH

INDIVIDUAL	NUMBER OF PAIRS OF SPOTS	NUMBER OF BODY PARTS WITH SPOTS	TOTAL BODY SURFACE	
			PERCENT OCCUPIED BY SPOTS	($mm.^2$)
1	5	5	0.19	563
2	6	6	.15	431
3	6	6	.16	422
4	6	6	.16	467
5	6	6	.20	470
6	6	6	.20	473
7	6	6	.22	475
8	6	6	.25	439
9	6	6	.26	446
10	7	7	.35	515
Means	6	6	0.21	470

antennal crescents were found. Each female possessed a pair of fenestrae on the cervical membrane just anterior to the first prosternal plate and additional pairs on the dorsal surface of the mesothorax, metathorax and second and third abdominal segments. One individual lacked fenestrae on the first abdominal tergum and another female differed from all the others in having a small pair of fenestrae on the fourth abdominal segment.

The variability of the males makes it difficult to compare the data obtained from them with that for males of other species. However, a comparison of the means for the group given in Table I with those published earlier for males of twenty other species of Acridinae[2] (Slifer, 1953b, Table V) shows that ***Dociostaurus maroccanus*** falls below the average for its subfamily both in the number of pairs of spots which it possesses and in the percentage of the total body surface occupied by them. A similar comparison for the females leads to the same conclusion.

It is obvious from the data just presented that the Moroccan locust is an exception to the generalization made earlier, for the species

[2]In a recent and very comprehensive study Dirsh (1956) raises the former tribe Truxalini of the Acridinae to subfamily status. According to this system of classification *Dociostaurus maroccanus* becomes a member of the subfamily Truxalinae.

studied up to that time, that grasshoppers and locusts which occur in very large numbers and do great damage to crops have especially well-developed spot patterns (Slifer, 1953b). At that time it was also pointed out that there is a highly significant correlation between body size and the number of pairs of specialized areas. Large species tend to have a high number of spots and small species to possess fewer. Among all of the species of Acrididae examined so far the Acridinae tend to be smaller in size than do the members of the other subfamilies. Moreover, the Acridinae often have a thinner body wall than do species which belong to other subfamilies. Specialized heat-sensitive areas would almost certainly be more useful to a large, heavy-walled insect than they would be to a small, thin-walled one, such as the Moroccan locust, where heat could be either transmitted through or absorbed by any part of the surface very quickly.

As stated above, dried museum specimens of *Dociostaurus brevicollis*, *Dociostaurus genei*, *Notostaurus anatolicus* and *Chorthippus albomarginatus* were also examined. A single male and a single female of each species was dissected. Antennal crescents were absent in all of the eight individuals just as they had been in the Moroccan locust. Prothoracic (cervical) fenestrae were present in each of the females and absent in each of the males. *Dociostaurus maroccanus* females, it will be recalled, all possessed fenestrae in this region but four of the ten males lacked them. The total number of fenestrae varied from eight to nine pairs in the females and from four to seven pairs in the males. These four species, then, possess patterns of heat-sensitive spots which are similar, in general, to those of the Moroccan locust.

If, as earlier work has indicated, these specialized areas of the body wall are of value to locusts and grasshoppers in helping them to alter their behavior quickly when the temperature of their environment changes then the question arises as to how the Moroccan locust succeeds so well with only a few small ones. Is the explanation that small, thin-walled species have less need of special areas through which alterations in temperature can be detected rapidly sufficient? Does *Dociostaurus maroccanus* have some other way of detecting temperature changes? Exact information on the rate at which heat is transmitted or absorbed by the various regions of the body wall of the living locust must be obtained before it is possible to decide whether the speculations concerning the function of the antennal crescents and fenestrae, which have been presented in this and the preceding papers, are sound or whether they must be modified.

Summary

1. *Dociostaurus maroccanus* (Thunberg) differs from the species of plague locusts and grasshoppers studied earlier in that the specialized, heat-sensitive areas present in its body wall are relatively small and few in number.

2. *Dociostaurus brevicollis* (Eversmann), *Dociostaurus genei* (Oesk.), *Notostaurus anatolicus* (Krauss) and *Chorthippus* (DeGeer), all of which are close relatives of *Dociostaurus maroccanus*, were examined. Their heat-sensitive areas are of the same general pattern as those of the Moroccan locust.

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1953b. The pattern of specialized heat-sensitive areas on the surface of the body of Acrididae (Orthoptera). Part II. The females. Trans. Amer. Ent. Soc. 79: 69–97.

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FIFTH ANNUAL MEETING ENTOMOLOGICAL SOCIETY OF AMERICA MEMPHIS, TENNESSEE, DECEMBER 2–5, 1957

The program for this meeting will be found in the September 1957 issue of the BULLETIN OF THE ENTOMOLOGICAL SOCIETY OF AMERICA.

THE CHARACTERIZATION OF INSECTS AND TICKS BY THEIR FREE AMINO ACID PATTERNS[1]

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Previous investigations in this laboratory have shown that mosquito extracts contain 19 free amino acids, the concentrations of which vary quantitatively from species to species as well as from stage to stage (Micks and Ellis, 1951, 1952). Subsequent evidence has demonstrated that paper chromatograms of amino acids in mosquito tissues may be used to distinguish between closely related species (Micks, 1954). More recently, paper chromatography was used as a systematic tool to compare several representatives of three orders of insects (Micks, 1956). Although there was evidence of qualitative differences in amino acids from order to order, most of the interspecific differences were on a quantitative basis.

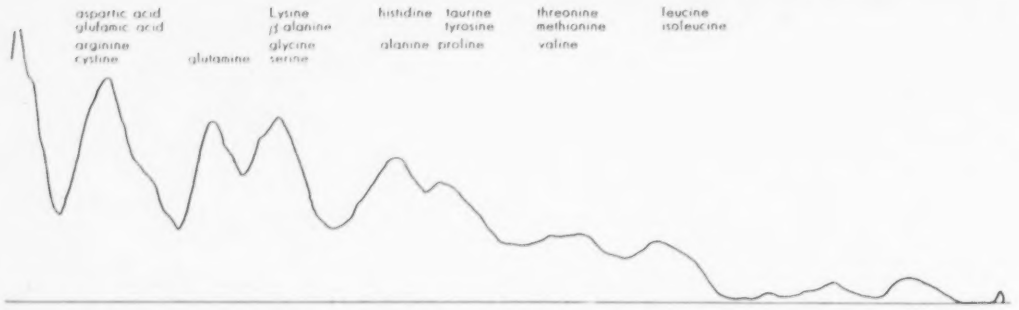

FIG. 1. Density curve obtained from a one-dimensional chromatogram of two female specimens of *Culiseta inornata*.

Since the completion of these studies, our techniques have been improved and extended to a variety of insect and tick species. The present report presents some of the results obtained during the past year and a half, using quantitative chromatographic methods to study amino acid patterns.

MATERIALS AND METHODS

Twenty-seven strains and species of arthropods belonging to four orders were studied: *Aedes aegypti* (L.) (Texas), *Aedes aegypti* (Mexico), *Aedes sollicitans* (Wlk.), *Aedes taeniorhynchus* (Wied.), *Aedes polynesiensis* Marks, *Culex pipiens* L., *Culex fatigans* Wied., *Culex molestus* Forsk., *Culex tarsalis* Coq., *Culiseta inornata* (Will.), *Psorophora ciliata* (F.), *Psorophora confinnis* (L.-A.), *Anopheles quadrimaculatus* Say (Texas), *Anopheles quadrimaculatus* (Mexico), *Anopheles albimanus* Wied., *Anopheles aztecus* Hoffman, *Triatoma gerstaeckeri* (Stål), *Triatoma infestans* (Klug), *Dermacentor andersoni* Stiles (Canada), *Dermacentor variabilis* (Say) (Massachusetts), *Dermacentor variabilis* (Florida), *Dermacentor variabilis* (Canada), *Dermacentor albipictus* (Pack.) (Canada), *Blattella germanica* (L.), *Supella supellectilium* (Serv.), *Periplaneta americana* (L.) and *Periplaneta brunnea* Burm.

The method of preparing chromatograms of the smaller specimens (mosquitoes, tick eggs and larvae) was a modification of that used by Hadorn and Mitchell (1951). Following anesthetization, specimens of like species and sex were enclosed in a small piece of gauze cloth and tied with a string. The material was placed in boiling distilled water for two minutes. Each specimen was touched lightly to a piece of blotting paper and crushed on the chromatographic paper with a flat-ended glass rod. Four adult female mosquitoes or an equivalent quantity of tick eggs and larvae were used to make a single preparation. The spot produced by each specimen was dried with a hair-dryer before adding the next in order to keep the spot as small as possible. Wings and legs were removed from the large insects (bugs and cockroaches) after boiling and were placed in a 10 ml. syringe. These specimens were crushed by pressure of the plunger and the tissue fluids added directly to the chromatogram paper through a 27 gauge needle.

All species were compared using duplicate one-dimensional chromatograms repeated several times. Whatman 3 mm. filter paper, cut into 9" x 11" sheets was employed throughout. The

[1]This investigation was supported by a research grant from the Robert A. Welch Foundation. Accepted for publication May 28, 1957. Paid paper.

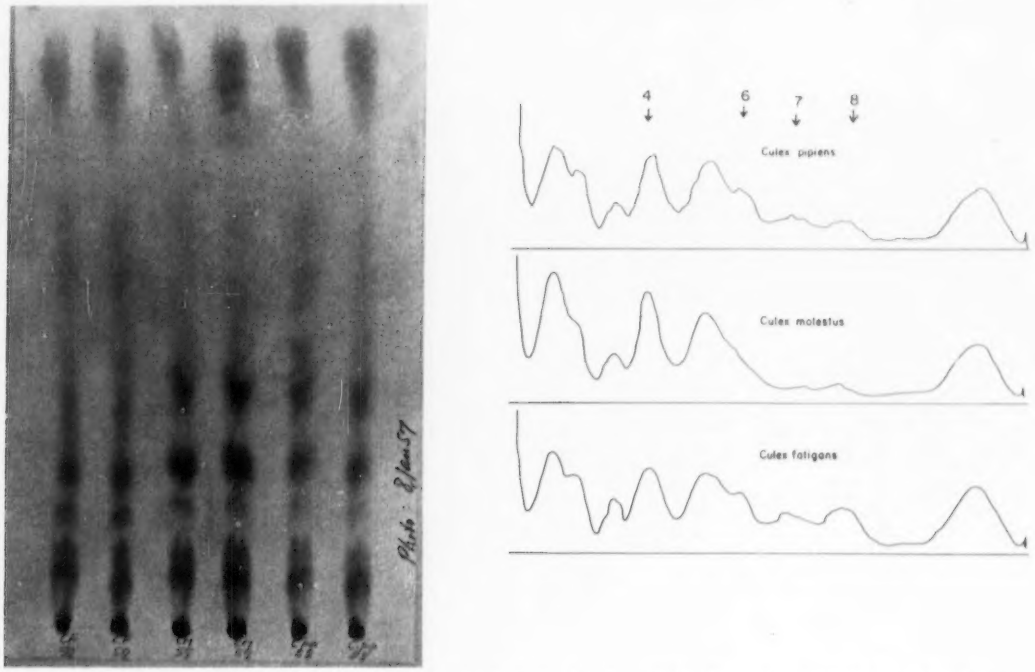

FIG. 2. Photograph of duplicate chromatograms of *Culex fatigans* (CF), *C. molestus* (CM) and *C. pipiens* (C. pip) and density curves obtained from one of each pair of chromatograms.

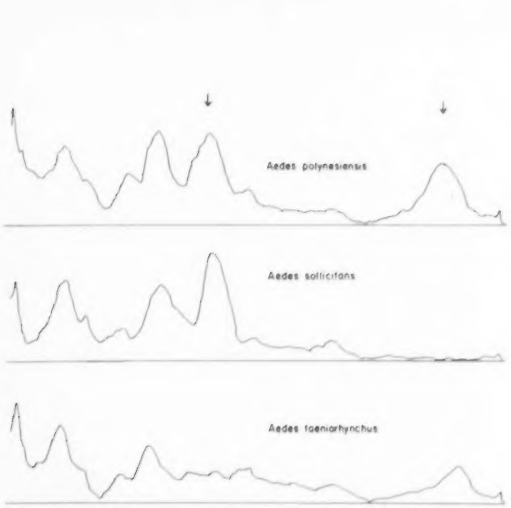

FIG. 3. A comparison of density curves from three species of *Aedes*.

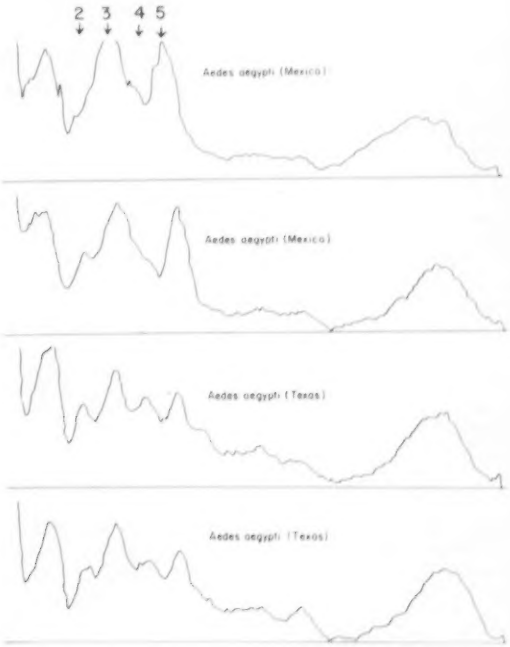

FIG. 4. Duplicate density curves of two strains of *Aedes aegypti*. Note the reproducibility of the curves.

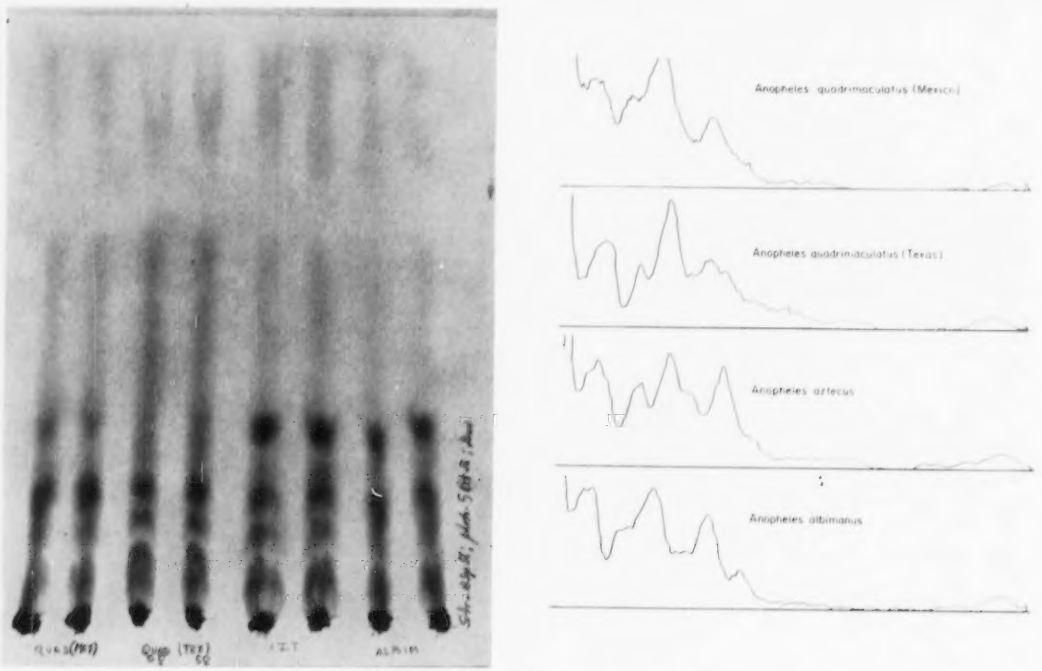

FIG. 5. Photograph of duplicate chromatograms of *Anopheles quadrimaculatus* (Mexico), *A. quadrimaculatus* (Texas), *A. aztecus* and *A. albimanus* (from left to right) Amino acid curves from these species are shown at theright.

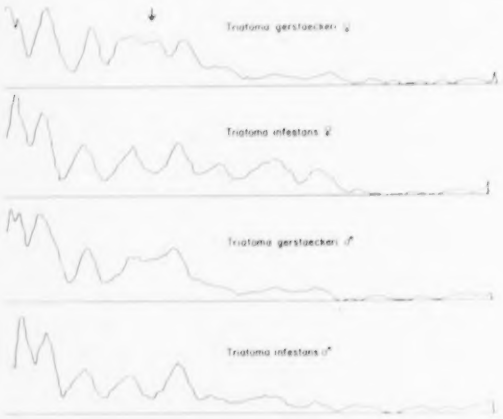

FIG. 6. A comparison of density curves of male and female specimens of *Triatoma gerstaeckeri* and *T. infestans*. Each curve was obtained from a single specimen.

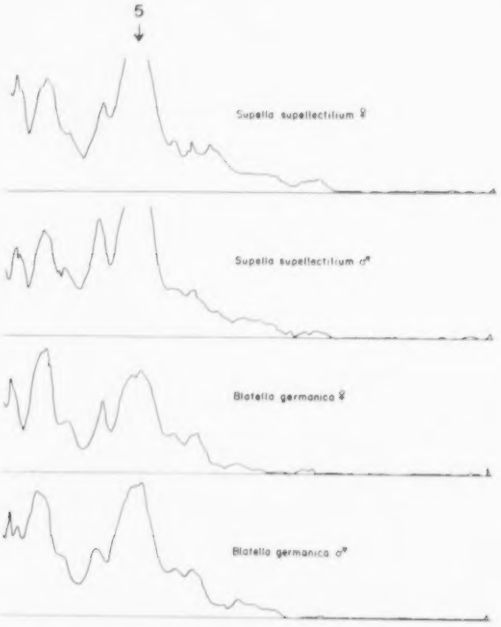

FIG. 7. A comparison of curves from males and females of two species of cockroaches.

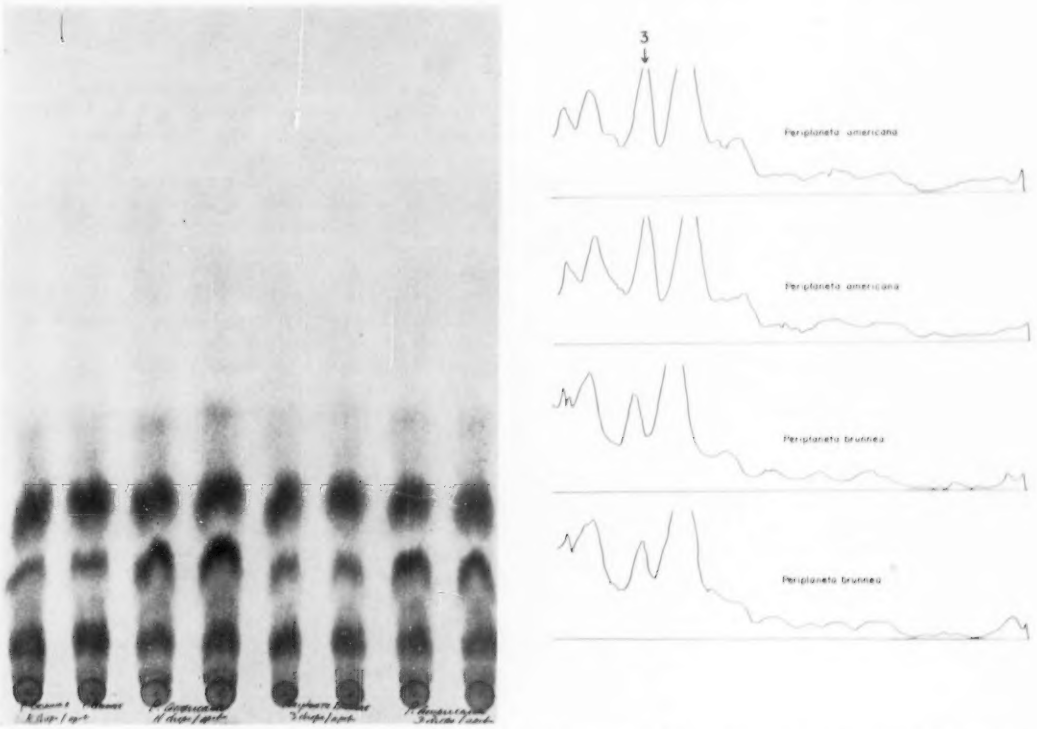

FIG. 8. Photograph of duplicate chromatograms of *Periplaneta brunnea* (1, 2, 5 and 6) and *P. americana* (3, 4, 7 and 8). The first four chromatograms were made with 4 drops of tissue fluid per spot and the others with 3 drops per spot. Duplicate density curves of each species are compared at the right.

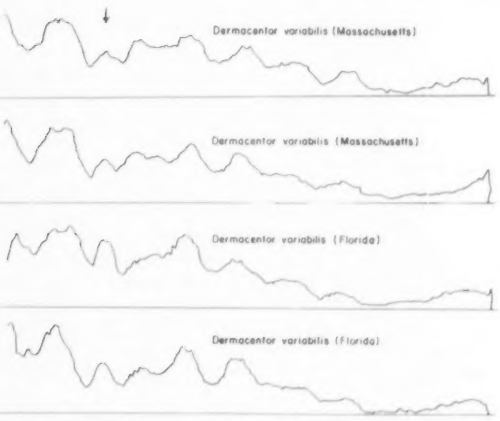

Figure 9. Comparison of duplicate curves from two strains of ticks.

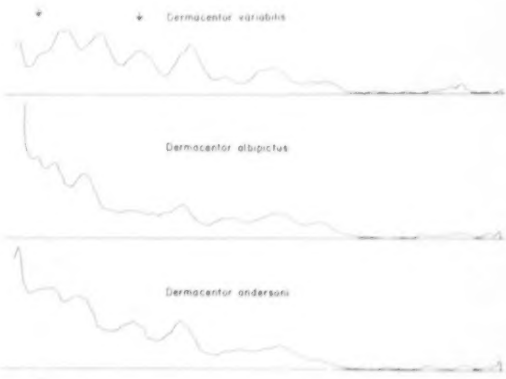

FIG. 10. Density curves of amino acids of three species of tick larvae.

chromatograms were fastened into cylinders using cellophane tape. Propanol-diethylamine-water (85:4:15) was used as the solvent which required approximately 9 hours to reach the top of the paper. In a few instances where two-dimensional chromatograms were prepared, butanol-acetic acid water (4:1:1) was used as the second solvent. The sheets were hung in a cabinet equipped with a small exhaust fan and allowed to dry after which they were sprayed with ninhydrin (0.2%) in water-saturated butanol, using a nasal atomizer. Approximately twelve hours after development of the sheets they were photographed and each chromatogram was cut into a separate strip. Each strip was run through a Photovolt transmission densitometer to obtain a maximum density curve of the free amino acids. Chromatograms and density curves obtained from the different species were compared to ascertain differences in amino acid concentrations.

RESULTS

Marked quantitative differences in the concentrations of free amino acids were observed between all genera and species of the four orders studied. Fig. 1 shows a density curve and the corresponding positions of the 19 amino acids which produced the density peaks in all one-dimensional chromatograms obtained in this study. A chromatographic comparison of three members of a closely related group of mosquitoes (*Culex pipiens, Culex molestus* and *Culex fatigans*) revealed quantitative differences as indicated by comparing density peaks 4, 6, 7 and 8 (fig. 2). *C. molestus* contained less taurine, tyrosine, leucine and isoleucine than the other species. Density curves from three species of *Aedes* (*polynesiensis, sollicitans* and *taeniorhynchus*) are shown in fig. 3. The arrows indicate the major points of difference. Different strains of the same species also presented somewhat different chromatograms. For example, duplicate density curves of our laboratory-reared *Aedes aegypti* were compared with those obtained from *A. aegypti* from Mexico (fig. 4). Density peaks 2, 3, 4 and 5 in the Texas strain are represented by only three peaks in the other strain. Furthermore, the yellow spot representing the amino acid, proline, was consistently darker in the Texas strain. Quantitative differences between the amino acid patterns of *Anopheles quadrimaculatus* (Mexico), *A. quadrimaculatus* (Texas), *Anopheles azteeus* and *Anopheles albimanus* are clearly shown in fig. 5. The accompanying curves likewise demonstrate that no two species are alike.

Curves obtained from the chromatograms of two species of *Trialoma* are seen in fig. 6. The males and females of *gerstaeckeri* are easily distinguished from those of *infestans* by comparing the part of the curves beneath the arrow. The sexes of *gerstaeckeri* present extremely similar chromatograms whereas the females of *infestans* have higher density peaks representing threonine, methionine, valine, leucine and isoleucine.

Some representatives of still another order (*Orthoptera*) are compared in the next two figures. Density curves of *Supella supellectilium* were easily differentiated from those of *Blattella germanica* by comparing peak number 5 which is much higher in *Supella* (fig. 7). This difference holds for both sexes of the two species. Duplicate chromatograms and corresponding curves from two species of *Periplaneta* were also compared (fig. 8). It can readily be seen that peak number 3 is much higher in *americana* than in *brunnea*. This striking difference between the two species is clearly evident in the accompanying photograph. *P. americana* also exhibited a more dense proline (yellow) spot than brunnea, although it is not shown clearly in either the photograph or the curves due to its color.

A chromatographic comparison was made of several strains and species of ticks belonging to the genus *Dermacentor*. Fig. 9 shows duplicate density curves derived from chromatograms of the eggs of two strains of *D. variabilis* from Massachusetts and Florida. The curves are essentially the same except for minor quantitative differences indicated by the arrow. The larvae of three species of *Dermacentor* could be separated on the basis of their density curves (fig. 10). The major differences occurred in the first few peaks shown at the left.

DISCUSSION

Perhaps the most striking feature of the results is the high degree of reproducibility of the amino acid patterns of each species studied. This may be due in part to the fact that insects contain comparatively large amounts of amino acids and therefore, minor quantitative differences between individuals of a given species are masked or otherwise inapparent. The density curves confirm and accurately quantitate the differences already apparent by visual comparison of one-dimensional chromatograms.

Each of the density peaks is produced by two or more amino acids except glutamine, which generally appears as a separate spot. The identity of the uppermost spot, which is particularly prominent on chromatograms of mosquitoes, is not known, but is thought to be a peptide. At the level of concentration used, it does not appear in chromatograms of cockroaches, bugs or tick larvae.

Striking quantitative differences between chromatograms representing different orders were noted. For example, most of the cockroaches studied contained a heavier concentration of the spot representing lysine, B-alanine, glycine and serine, than representatives of the other orders.

Furthermore, the triatomid bugs and the ticks consistently contained less of several of the amino acids which appear below the threonine, methionine, valine spot on the chromatograms.

Quantitative differences in the amino acid patterns of species belonging to the same genus usually involved several amino acids. However, it was interesting to note that chromatograms of *P. brunnea* and *P. americana* were practically identical except that the latter species exhibited a markedly higher glutamine content. Whereas chromatographic differences between two strains of *D. variabilis* were small, strains of *A. aegypti* as well as strains of *A. quadrimaculatus* could easily be distinguished on the basis of quantitative differences in several amino acids. Males and females of a given species presented essentially the same pattern of amino acids.

SUMMARY

Quantitative chromatographic methods were used to compare the free amino acid patterns obtained from 27 strains and species of mosquitoes, triatomid bugs, cockroaches and ticks. One-dimensional chromatograms and density curves obtained therefrom were found to be completely reproducible for each species studied. Marked quantitative differences in amino acid concentrations were observed between all genera and species of the four orders studied. These differences usually involved several amino acids although two species belonging to the same genus appeared to differ only in their content of a single amino acid. In most instances, different strains of the same species presented considerably different amino acid patterns.

ACKNOWLEDGMENTS.—The authors extend their sincere appreciation to Dr. L. E. Rozeboom and Dr. Eulogio Bordas for supplying certain strains of mosquitoes. Thanks are also due Mr. Jack Gregson and Dr. Carroll Smith for sending specimens of ticks.

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THE ADULTS AND IMMATURE STAGES OF AEDES MUELLERI DYAR (DIPTERA: CULICIDAE)[1]

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Aedes (*Ochlerotatus*) *muelleri* Dyar, 1920 is one of the rarer North American mosquitoes. Up to 1956 only four specimens, two of each sex, had been reported in the literature and nothing had been published regarding the immature stages or breeding places of this species. Dyar (1920: 81–2) described *muelleri* from one male and one female collected in Mexico City by Juan Müller. He twice described (Dyar, 1922a: 92–3; 1922b: 55) as new *Aedes iridipennis* from a single female collected in the Chiricahua Mountains, Arizona by C. H. T. Townsend, and later (Dyar, 1928: 172) synonymized it with *muelleri*. Martini (1935: 51) reported a second male, identified on the basis of the genitalia, from Chapingo, Federal District, Mexico.

In August, 1954 the author took a single female of *muelleri*, biting, at Madera Canyon in the Santa Rita Mountains, Santa Cruz County, Arizona. This record was cited by Richards *et al* (1956: 14). A second visit to the same locality in August, 1955 disclosed this species breeding in tree holes in association with *Aedes* (*Kompia*) *purpureipes* Aitken, 1941 (McDonald, 1957), *Aedes* (*Ochlerotatus*) *monticola* Belkin and McDonald (1957) and *Orthopodomyia signifera* (Coquillett, 1896). On August 4, 1956, while searching for topotypic *Aedes varipalpus* (Coquillett, 1902) near Williams, Coconino County, Dr. John Belkin and the author were surprised to find *muelleri* larvae and pupae mixed with and greatly outnumbering *varipalpus* in small rot holes in the dominant oak of that region, *Quercus gambelii* Nutt. On the same date a single larva of *muelleri* was found with several *varipalpus* in a similar rot hole in the Hualpai Mountains of Mohave County, 100 miles to the west.

The previously unknown larva and pupa and the poorly known adults of the Madera Canyon population of *muelleri* are described here to supplement the recently published *Mosquitoes of North America* (Carpenter and La Casse, 1955). Belkin's (1953a, b) systems of chaetotaxic nomenclature and presentation of hair branching data are used here without change.

I wish to thank Dr. John N. Belkin and Dr.

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Alan Stone for comparing the Arizona specimens with Dyar's types at the U. S. National Museum and for reading the manuscript. The identification of *Quercus gambelii* was made by Dr. Cornelius H. Muller of Santa Barbara College, University of California.

AEDES (OCHLEROTATUS) MUELLERI Dyar

1920. *Aedes (Heteronycha) muelleri* Dyar, Insecutor Inscit. Menstr. 8: 81–2; Mexico City, Mex.; type ♂, type ♀ [USNM, No. 22826].
1922. *Aedes iridipennis* Dyar, Insecutor Inscit. Menstr. 10: 92; Chiricahua Mts., Ariz.; type ♀ [USNM, No. 25264].
1922. *Aedes (Heteronycha) iridipennis* Dyar, Proc. U. S. Nat. Mus. 62: 55.
1928. *Aedes (Ochlerotatus) muelleri* Dyar, Mosq. of Americas, p. 172.
1932. *Aedes (Ochlerotatus) muelleri*, Edwards, Gen. Insectorum, p. 145.
1935. *Aedes (Ochlerotatus) muelleri*, Martini, Mosq. de Mexico, p. 51.
1950. *Aedes (Gualteria) muelleri*, Vargas, Rev. Inst. Salubr. y Enferm. Trop. 11: 62.
1955. *Aedes (Ochlerotatus) muelleri*, Carpenter and La Casse, Mosq. of North America, p. 206.

DESCRIPTION

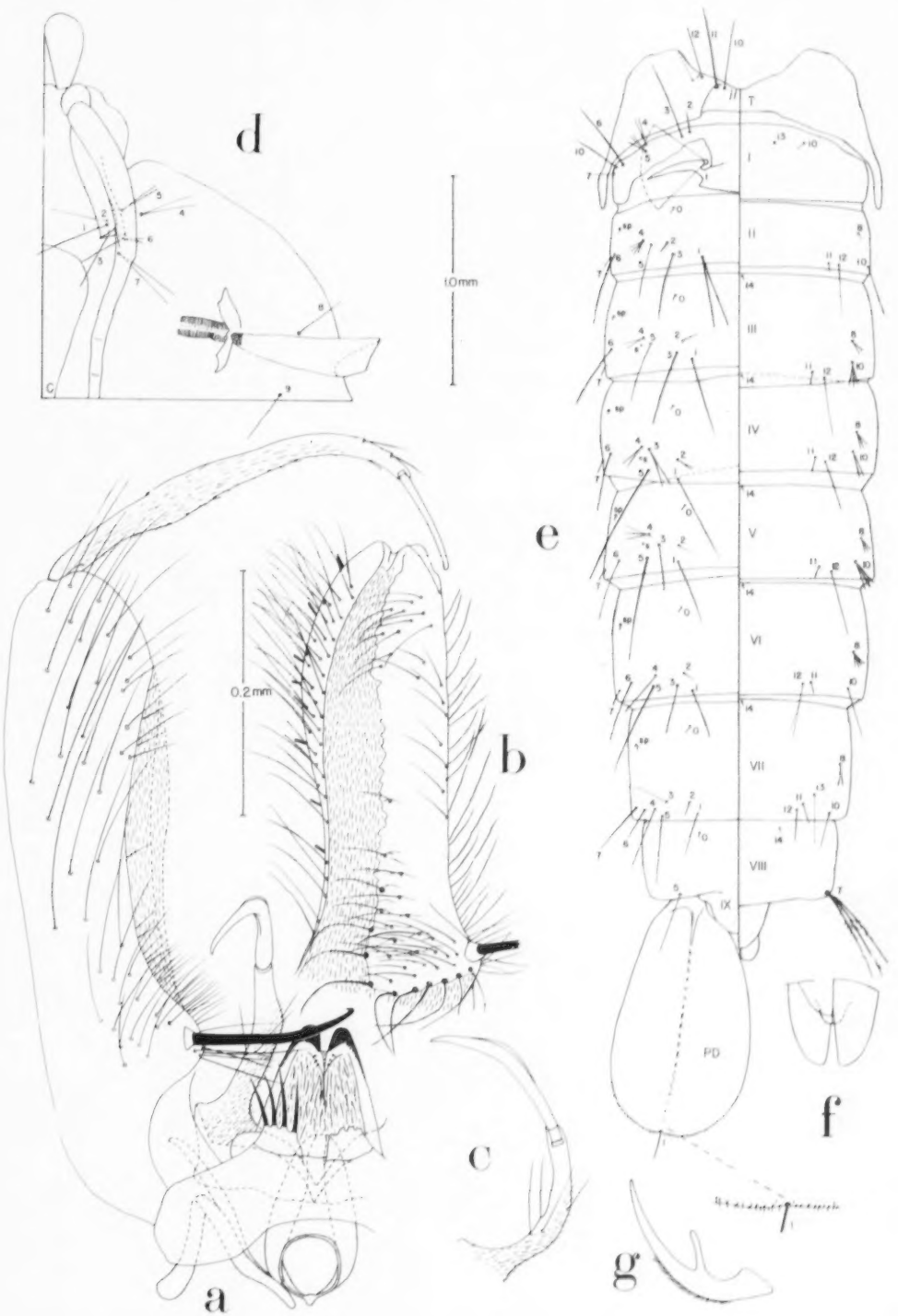
FEMALE.—*Wing* about 3.50–3.90 mm. *Proboscis* dark-scaled. *Palpus* about 0.17 proboscis; dark scaled. *Antenna* with black integument; torus and first flagellar segment each with a patch of broad white scales. *Vertex* with broad median white stripe of large appressed lanceolate scales, submedian dark spot, lateral white patch of broad decumbent scales contiguous over eye with median stripe, and ventrolateral dark area which includes white and dingy-white scales; vertical and occipital erect forked scales numerous and extensive, white on median stripe, dark caudad of submedian spot. *Scutum* with black integument; a white median stripe of narrow lanceolate scales, often appearing as two narrow lines enclosing acrostichal bristles, extending to prescutellar space; a subequal or broader black submedian stripe of narrow decumbent lanceolate scales extending to scutellum; fossa mainly with white broad lanceolate scales mixed with black scales posteriorly; supraalar area with narrow line of white scales dorsally which connects with white scales of fossa, laterad of this a large, usually dark-scaled area (rarely with predominantly white scaling) which expands anteriorly, is naked posteriorly and is bordered laterally by lanceolate white scales from scutal angle to wing base; prescutellar space bordered by broadly lanceolate white scales. *Scutellum* with large median patch of broadly lanceolate white scales and small white patches on lobes. *Pleuron* densely clothed with broad white decumbent, appressed or erect scales, posterior scales the largest, scales of *ppn* and especially *apn* sometimes narrowly lanceolate; *ppn* with quite variable amount of dark scaling dorsally; hypostigial scale patch well developed; small dorsal scale tuft on postcoxal area; scales of *me* usually extend to lower margin; *ustp* and *lstp* patches usually narrowly separated, the former barely contiguous with *pa* patch and merging with *psp* patch which is usually contiguous with hypostigial patch; metameron with small dense scale patch; pleural setae white or yellowish, present as follows: *apn* 20–25, *ppn* 10–15, *ppl* 10–20, *stp* 10–20, *ume* 20–30, *lme* (absent), *pa* 10–20, *psp* 5–10. *Paratergite* white-scaled ventrally. *Wing* completely dark-scaled; scales linear on dorsum of R_s, R_{2+3}, R_2 and R_3, narrow on M and 1A, broad elsewhere on dorsum; a small patch of black scales at base of 1A ventrally. *Halter* light-scaled. *Legs* generally purplish metallic black with white scaling as follows: knee spots conspicuous, restricted to femora; femora circled with white at base, white-scaled posteriorly to apex on fore femur, becoming black distally, with apical white ring weakest on foreleg; tibiae and tarsi black; all claws simple. *Abdomen* largely black with narrow transverse basal white bands contiguous with lateral basal white patches, the latter largest on VI, VII; tergite I white in middle and laterally; tergite II with isolated median basal white patch; laterotergite white-scaled; sternites predominantly white with median apically-expanded black scale patches; segment VIII not completely retractile. Specimens examined: 10.

MALE.—Coloration in general as in female with the following exceptions: dark scales absent on fossa and *ppn;* narrow lanceolate black scales of supraalar area replaced almost entirely by white scales; vertex with few or no black appressed scales. *Palpus* slightly shorter than proboscis. *Antenna* with penultimate segment about equal to 5 preceding segments, apical about 0.85 penultimate; scaling of torus reduced to several mesal white scales. Claws of fore- and mid-legs (fig. 1g) toothed; hind claws simple.

MALE GENITALIA (as in Fig. 1a).—Lobes of ninth tergite short, rounded, well-sclerotized, each bearing two to four strong setae. Proctiger with tenth sternite heavily sclerotized at apical hooks and along sides, usually with three small setae on membrane proximad of hook. Phallosome usually tapered towards apex, dorsal surface and sides well sclerotized. Claspette stem slender, spiculate to about distal third, bearing a slender

EXPLANATION OF FIGURES

FIG. 1. Male and pupa of *Aedes muelleri* Dyar; Santa Rita Mts., Ariz. (UCLA 173-2). *a*, Dorsal (morphologically) aspect of male genitalia, large lateral setae and scales of sidepiece not shown. *b*, Mesal aspect of left (morphologically) sidepiece, scales not shown. *c*, External aspect of left claspette. *d*, Ventral aspect of left anterior portion of cephalothorax of female pupa. *e*, Dorsal (left) and ventral (right) aspects of metanotum and abdomen of female pupa. *f*, Dorsal (left) and ventral (right) aspects of segment IX–X of male pupa. *g*, Lateral aspect of male mesothoracic claw.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seta at distal third on mesal margin (seen from dorsal aspect) and two or three similar setae dorsally before middle. Claspette filament slightly longer than stem, sickle-shaped or gently curved, expanded by thin ridge along curvature. Sidepiece (basistyle) four to five times median width in dorsal aspect, distal half swollen in mesal aspect; mesal two-thirds of dorsal surface with patch of short setae at base becoming longer, sparser and mixed with scales at middle; outer third of dorsal surface, external and ventral surfaces with usual strong bristles and scales; a smaller patch of short setae along membrane margin in distal fourth of dorsal surface; basal lobe moderately developed, bearing a very heavy apically-hooked differentiated seta on dorsal surface, ventrad a patch of short setae with long heavier setae on ventral margin; dorsal margin of membrane jagged and uneven, ventral margin smoother; apical lobe completely absent. Setae of sidepiece longer than shown in figure. Clasper (dististyle) with claw about two-thirds as long as sidepiece, swollen before middle, spiculate save at apex, bearing two or three small outer and one inner setae subapically; claw about one-fourth as long as clasper, slender, apex blunt and curved. Specimens examined: 10.

PUPA.—Linear measurements (in mm.; mean and observed range): Abdomen: ♂ 3.36 (3.10–3.52), ♀ 3.90 (3.60–4.10). Trumpet: ♂ 0.30 (0.28–0.31), ♀ 0.35 (0.32–0.36). Paddle: ♂ 0.50 (0.46–0.52), ♀ 0.52 (0.50–0.55). Specimens studied: 10 skins (5♂, 5♀).

Cephalothorax (Fig. 1d, e): Lightly pigmented, darker between trumpets and on metanotum. Trumpet lightly pigmented, darker in area of well-developed tracheoid; gently tapered from tracheoid, length five to seven times median width; pinna less than distal fourth, slit lacking; median reticulations faint, shingle-like; patch of distal subhexagonal reticulations usually well developed. Relative position, length and degree of development of hairs as figured. Hair 1(1), 2(1; 1.05; 1–2), 3(1), 4(2, 1; 1.60; 1–3), 5(2; 2.15; 2–3), 6(2; 2.00; 1–3), 7(2, 3; 2.26; 1–4), 8(1; 1.20; 1–3), 9(1), 10(1), 11(1; 1.06; 1–2), 12(1). An anomalous hair (1, 2; 1–5) is occasionally seen on the mesal surface of the wing case, rarely on both sides of the pupa; this hair also occurs in ***purpureipes*** and ***monticola***. One skin shows an anomalous hair laterad of 12–T and identical to that seen in ***monticola***.

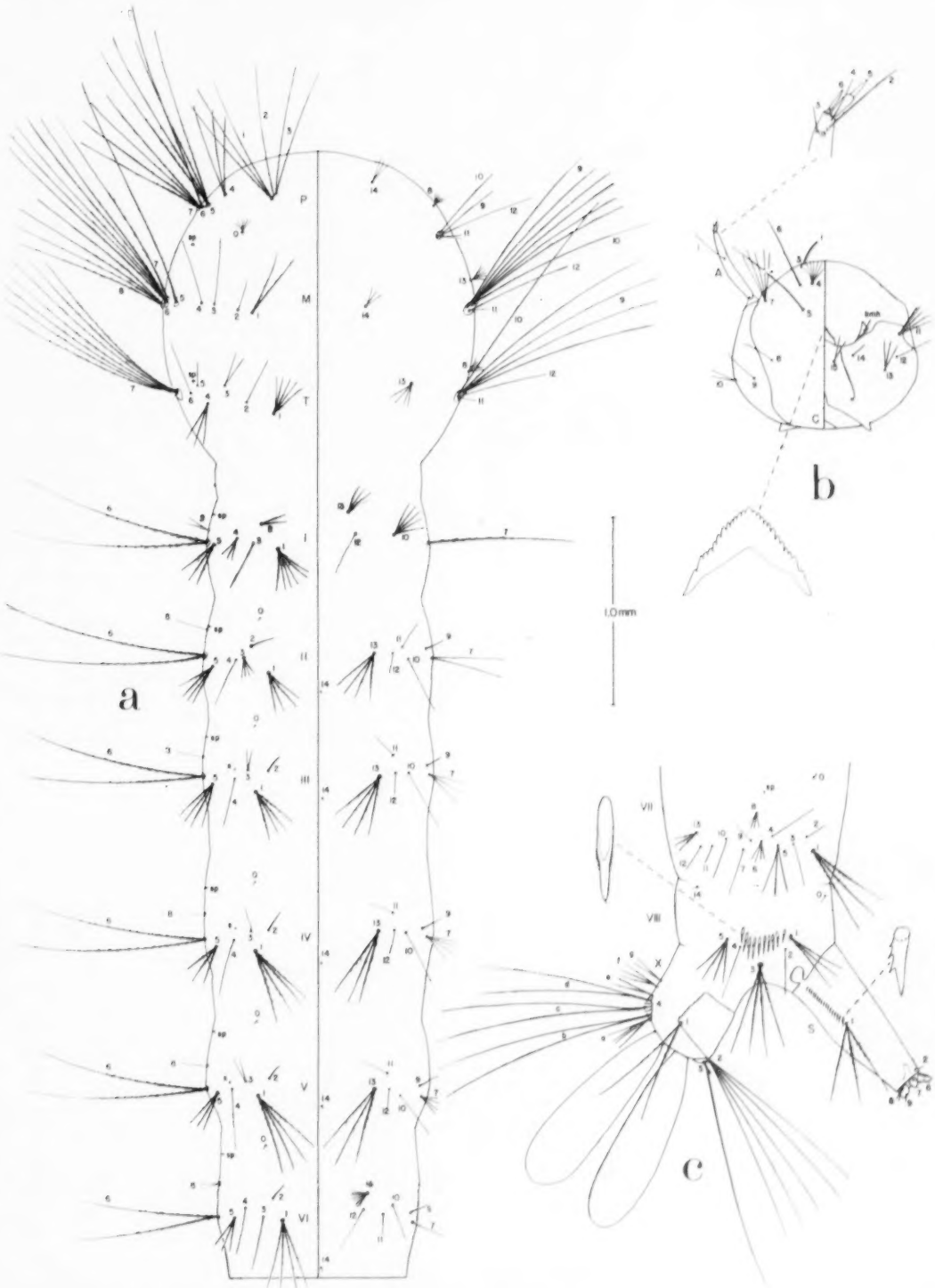
Abdomen (Fig. 1e): Lightly pigmented, darkest on I, progressively lighter through IV; V–IX and paddle uniformly light yellowish brown; anteromedian ventral area of III very dark, similar lighter areas on IV, V. Rudimentary spiracles of II–VII large, well-sclerotized, that of I large, usually covered by metanotum in mounted skins. Dorsal sensilla present on III–V. Segment I: reticulations between float hairs small, indistinct to well-developed; hair 1(30–110 branches), 2(1), 3(1), 4(2, 3; 2.20; 2–4), 5(3, 2; 2.45; 2–5), 6(1), 7(1), 10(1; 1.05; 1–2). Ventrally, an anomalous hair (1, 2, 3; 2.45; 1–5) and a more mesal peglike seta are often present (see McDonald, 1957). Segment II: hair 0(1; 1.05; 1–2), 1(2; 2.28; 2–4), 2(1), 3(1), 4(4, 3; 4.00; 3–6), 5(1; 1.15; 1–2), 6(1), 7(1), 8(1, 2; 1.33; 1–3), 10(1; 1.05; 1–2); hair 11 tiny, absent in 5 percent of cases; hair 12 fully developed or merely an alveolus, completely absent in about half of skins seen. Segment III: hair 0(1), 1(1, 2; 1.63; 1–3), 2(1), 3(1; 1.05; 1–2), 4(2, 3; 2.25; 1–4), 5(1), 6(1), 7(1), 8(2, 3, 4; 2.50; 1–4), 10(3, 2; 2.75; 1–4), 11(1), 12(1), 14(1). Segment IV: hair 0(1), 1(1), 2(1), 3(2; 2.05; 1–3), 4(2, 1; 1.80; 1–3), 5(1; 1.15; 1–2), 6(1; 1.05; 1–2), 7(1), 8(3, 2; 2.95; 2–4), 10(2, 1; 1.85; 1–4), 11(1), 12(1), 14(1). Segment V: hair 0(1), 1(1), 2(1), 3(1; 1.05; 1–2), 4(3–2, 4; 3.10; 2–6), 5(1), 6(1), 7(1), 8(3, 4, 2; 3.05; 1–5), 10(3, 2; 2.80; 2–4), 11(1), 12(1), 14(1). Segment VI: hair 0(1), 1(1), 2(1), 3(1), 4(1; 1.15; 1–2), 5(1), 6(1), 7(1), 8(4, 3; 3.45; 2–5), 10(1), 11(1; 1.05; 1–2), 12(1), 14(1). Segment VII: hair 0(1; 1.05; 1–2); 1(1), 2(1), 3(1), 4(1), 5(1), 6(1, 2; 1.45; 1–3), 7(1, 2; 1.47; 1–3), 8(2, 3; 2.50; 2–5), 10(1), 11(1; 1.05; 1–2), 12(1), 14(1); anomalous hair 13 present in one case. Segment VIII: hair 0(1), 5(1; 1.10; 1–2), 7(3, 2, 4; 3.25; 2–6), 14(1). Paddle: hair 1(1; 1.05; 1–2).

Variation: A female pupal skin from the vicinity of Mexico City (W. E. Snow, collector) shows the following departures from the preceding branching ranges which are based on ten Arizona pupae: hair 6-C(4), 10–C(2), 1–IV(2). No differences in position or relative size of hairs are apparent, nor does this pupa differ in pigmentation, sculpturing or shape of any structure. The usual variability in relative hair position is seen in this skin, an extreme case being the complete reversal in the position of hairs 4, 5-II on the left side.

LARVA.—Relative position, length and degree of development of hairs as figured. Drawing shows larva somewhat flattened. Specimens studied: 5. *Head* (Fig. 2b): Slightly wider than long (length includes collar); maximum width about 1.0 mm.; color uniform yellow brown; integument smooth; collar well-developed; width at collar about 0.45 mm. Mental plate as figured, with one strong median tooth and (9, 10; 9–13) distinct teeth on each side. Hair 0(1; tiny, slender, ventrolaterad of hair 3), 1(1; widened before middle; minutely barbed), 2(not present),

EXPLANATION OF FIGURES

FIG. 2. Fourth instar larva of *Aedes muelleri* Dyar; Santa Rita Mts., Ariz. (UCLA 173-2). *a*, Dorsal (left) and ventral (right) aspects of thorax and abdominal segments I–VI. *b*, Dorsal (left) and ventral (right) aspects of head. *c*, Left lateral aspect of terminal abdominal segments.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3(1), 4(7, 8; 5–9), 5(1), 6(1), 7(5–6; 4–7), 8(1), 9(1, 2; 1–2), 10(2; 2–3), 11(4–5–6; 4–7), 12(1), 13(3, 4; 3–5), 14(1), 15(2; 2–3), basal maxillary hair (fig. 2b, ***bmh***) (1). Antennal shaft about 0.40 mm., with several minute spicules along entire length; hair 1(1; 1–2), inserted beyond middle; basal sensillum present on proximal margin of sclerotized shaft; apical antennal hairs single.

Thorax (Fig. 2a): Integument smooth; rudimentary spiracles on M and T distinct; at positions figured. Hairs 5– to 7–P, 5– to 8–M, 7–T and pleural groups with sclerotized tubercles; 6, 7–M with common tubercle; tubercles of 5, 6, 7–P separate; 1– to 3–P and 6–T lacking alveolar plate. Heavier thoracic hairs weakly barbed. Prothorax: hair 0(6, 7; 5–9), 1(3; 3–4), 2(1), 3(2; 2–4), 4(3, 4; 3–4), 5(4, 3; 3–4), 6(1; 1–2), 7(4; 3–6), 8(7; 6–9), 9(1), 10(1), 11(2; 1–2), 12(1), 14(3; 2–3). Mesothorax: hair 1(2–3; 1–3), 2(1), 3(1), 4(1), 5(1), 6(5, 6; 4–6), 7(1), 8(6, 8; 4–8), 9(6, 5; 5–6), 10(1), 11(1, 2; 1–2), 12(1), 13(16; 13–19), 14(3; 3–4). Metathorax: hair 1(4–6;4–6), 2(1), 3(2, 3; 1–3), 4(3, 2; 2–3), 5(1), 6(1), 7(7; 7–8), 8(9, 6–7; 6–10), 9(4, 5; 4–5), 10(1), 11(1; 1–2), 12(1), 13(4; 3–5).

Abdomen (Fig. 2a, c): Integument smooth; hair 6 with small, poorly-sclerotized tubercle which is largest on I and dwindles to a trace on VI; dorsal sensilla present on III to V at or near positions figured. Segment I: hair 1(6, 5; 4–7), 2(2; 2–3), 3(1), 4(4–3; 3–6), 5(3, 4–5; 3–6), 6(2), 7(1), 8(absent), 9(2), 10(5, 9; 4–9), 11(absent), 12(1), 13(4, 5–7; 4–7), 14(absent). Segment II: hair 0(1), 1(4; 4–5), 2(1), 3(4, 5; 3–5), 4(1), 5(4–3; 3–5), 6(2), 7(2; 1–2), 8(1–2; 1–2), 9(1), 10(1), 11(1), 12(1; 1–2), 13(4; 4–5). Segment III: hair 0(1), 1(4), 2(1), 3(2; 1–2), 4(1), 5(4–5; 3–5), 6(2), 7(2–4; 2–4), 8(1; 1–2), 9(1), 10(1), 11(1), 12(1), 13(4, 3; 3–4), 14(1; 1–2). Segment IV: hair 0(1), 1(4; 4–5), 2(1), 3(1; 1–2), 4(1), 5(3; 2–5), 6(2), 7(4; 3–5), 8(1), 9(1), 10(1), 11(1), 12(1), 13(3–4; 3–4), 14(1). Segment V: hair 0(1), 1(4; 3–4), 2(1), 3(2–3; 2–3), 4(1), 5(3; 3–4), 6(2), 7(4, 3–2; 2–5), 8(1), 9(1), 10(1), 11(1), 12(1), 13(3; 3–4), 14(1). Segment VI: hair 0(1), 1(4; 3–4), 2(1), 3(1), 4(1), 5(3), 6(2), 7(1), 8(3, 4; 2–4), 9(1), 10(1), 11(1), 12(1), 13(10, 8; 7–10), 14(1). Segment VII: hair 0(1), 1(3–4; 3–4), 2(1), 3(1), 4(1), 5(3), 6(4; 3–4), 7(1), 8(4; 4–5), 9(1), 10(1), 11(1), 12(1), 13(3, 2; 2–4), 14(1). Segment VIII: comb scale thorn-shaped with long apical spine and short lateral spinules, its tip flattened, translucent, usually twisted; scales (10, 8; 8–12) in a single, slightly curved row; alveolus of I–VIII with almost colorless plate attached ventrally; hair 0(1), 1(3, 4; 3–5), 2(1), 3(4; 4–5), 4(1), 5(4; 3–4), 14(1). Siphon: gently convex dorsally, proximal half slightly concave ventrally, extreme apex not constricted; index (ratio dorsal length to median width) about 3.00 (all available examples flattened); color brown, darker distad of hair 1–S and along proximal margin; imbrications not seen; valves well sclerotized; distal pecten tooth attains 1–S; teeth (17–18; 14–18) well aligned, sinuous or staggered, individual tooth short, with two to four barbs along leading edge, distal barb often largest; acus constricted at base; hair 1–S at about 0.40; hair 1(3; 3–4; branches tend to constrict proximally), 2(1), 3(vestige of alveolus shows), 4 and 5(distinct alveoli), 6(1; surpasses dorsal valve), 7(1; indistinct), 8(2, 3; 2–3), 9(1), 10–13(all visible; not studied). Segment X: saddle incomplete, reaching about half across segment; pigmentation as in lighter areas of siphon, slightly darker in middorsal area; imbrications distinct; cephalic and caudal margins simple, ventral margin variably indented; dorsal and ventral gills subequal, longer than anal segment, slightly swollen (fig. 2c), rounded apically; hair 1(2; 2–3) about twice length of saddle, arising on margin slightly above ventrocaudal angle, alveolus not quite enclosed by margin; dorsal brush (hair 2, 3–X) arising on well-sclerotized tubercle, hair 2(5), 3(1; with characteristic short frayed barb on proximal leading edge in most specimens); ventral brush (hair 4a-g) with weakly-sclerotized cratal plate; 4a(short; 4–5; 4–5), 4b(long; 2), 4c(long; 2), 4d(long; 2–3; 2–3), 4e(short; 2, 3; 2–3), 4f(short; 3, 2; 2–4), 4g(short; 2; 2–3; one hair only); hair 4g and usually 4f free of cratal plate.

Variation: The northern Arizona (Williams, Hualpai) larvae were acquired too late to permit more than a gross inspection. All appear very close to the southern population but a sizable percentage show no proximal barb on hair 3–X of the dorsal brush, and hair 1–C is usually frayed at about the middle.

DISTRIBUTION

MEXICO.—Mexico: ***Mexico City***, date?, ♂, ♀ (Juan Müller) [USNM; Dyar, 1920–81]; ***Tlalnepantla***, elev. *ca.* 7,600′, XI–10–1955, 1♀, pupa, "maguey" (W. E. Snow) [USNM; Snow, 1956, *in lit.*]; ***Chapingo***, VI–29–1924, 1♂ (collector?) [ENCB?; Martini, 1935: 51].

ARIZONA.—Cochise County: ***Indian Creek***, Chiricahua Mts., elev. 6,100′, VIII–17–1917, 1♀, "biting by day in cave" (C. H. T. Townsend) [USNM; Dyar, 1922a: 92]. Santa Cruz County: ***Madera Canyon***, Santa Rita Mts., elev. *ca.* 6,500′, VIII–25–1954, 1♀, biting at noon (W. A. McDonald) [UCLA]; elev. *ca.* 5,500′, VIII–17–1955, 14♂, 13♀, pupae, larvae, tree holes (W. A. McDonald) [USNM, BMNH, CAS, UCLA]. Coconino County: ***Williams***, Bill Williams Mt., elev. *ca.* 7,000′, VIII–4–5–1956, 46♂, 63♀, pupae, larvae, tree holes (J. N. Belkin and W. A. McDonald) [USNM, BMNH, ENCB, CU, UCD, UCLA]. Mohave County: ***Hualpai Mts.***, elev. *ca.* 6,500′, VIII–4–1956, larva (this record possibly due to contamination by Williams collections) (J. N. Belkin and W. A. McDonald) [UCLA].

This species probably exhibits a fairly continuous range from central Mexico northward through the Sierra Madre Occidental to the Grand Canyon of Arizona, wherever rainfall is sufficient to permit tree hole breeding.

BIONOMICS

A single female of ***muelleri*** was collected in August, 1954 biting at noon in the shade of pine trees, about two miles up the footpath from the end of the Madera Canyon road. This location was revisited in August, 1955 but neither specimens nor likely breeding sites were found. Numerous oaks occur nearby at lower elevations, however.

In August, 1955 a single male pupa of ***muelleri*** was siphoned from a rot hole in a dead sycamore log in which *Aedes* ***monticola*** predominated, about 1 mile down-canyon from the Santa Rita Lodge. The remainder of the adults (13♂, 13♀) were reared from larvae and pupae found in a rot hole in a living oak at the upper end of the Madera Canyon Road. A single larva of ***monticola*** occurred here as well.

At Williams the water in most of the cavities was very dark and the temperature of one hole was 19°C. at noon. No adults of ***muelleri*** were collected in the field on the 1956 trip, although females of ***varipalpus*** and *Aedes* (*Ochlerotatus*) ***trivittatus*** (Coquillett, 1902) were blooded in the immediate area.

The two northern Arizona collections were made in a zone of *Quercus gambelii* Nutt. mixed with the lower-limit *Pinus* sp.; the Madera Canyon site is similar but with a different species of oak (not identified) supporting ***muelleri*** and with sycamore occurring nearby.

Of great interest is a recent collection made by Dr. W. E. Snow (1956, *in lit.*) who informs me that he reared a female of ***muelleri*** from dry material found in the axils of "***maguey***" (Agave?) near Mexico City.

TAXONOMIC DISCUSSION

Belkin and McDonald (1957) discuss the probable affinities of this species with the ***pulchritarsis-varipalpus*** group of *Ochlerotatus*. They also provide additions to the keys of Carpenter and La Casse (1955) for the separation of the male genitalia and larva of ***muelleri***.

The fact that the Arizona and Mexico populations of ***muelleri*** are separated by a distance of roughly 1,000 air miles draws attention to the paucity of mosquito records from northwestern Mexico. When adequate male material becomes available from intermediate areas, the Arizona ***iridipennis*** may possibly prove morphologically distinct from the Mexican ***muelleri***.

Specimens of the Arizona populations have been deposited at the U. S. National Museum [USNM], the British Museum (Natural History) [BMNH], the Escuela Nacional de Ciencias Biologicas [ENCB], Cornell University [CU], the California Academy of Sciences [CAS] and the University of California (Berkeley, Davis, Los Angeles) [UCB, UCD, UCLA].

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BLACK FLIES OVER LAKES (SIMULIIDAE, DIPTERA)[1]

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Few observations of the activity of adult black flies over the water have been reported. Therefore the following observations of species that were collected over water are of interest. Many black flies were flying over the water at 8:30 a.m. (E.S.T.) on May 27, 1955, while we were travelling in a canoe in the middle of Lake Sasajewun, Algonquin Park, Ontario. Eight females were netted and identified as *Simulium* (*Eusimulium*) *euryadminiculum* Davies,[4] a species known to feed on domestic ducks (*Anas* sp.) but not on mammals (Anderson 1956, Davies and Peterson 1956, Fallis 1956). At 8:00 p.m. on May 31, 1955, five females of *S. euryadminiculum* and one *Simulium* (*Simulium*) *venustum* Say were netted from a motor boat on Lake Opeongo, Algonquin Park, 300–400 yards from shore. On June 4, *S. euryadminiculum* females were numerous from 6:00–7:00 p.m. over mid Lake Sasajewun, but scarce by 8:00 p.m.

To determine the diurnal and seasonal change in the number of flies over the water, a standard "netting" procedure was started on the morning of June 7, 1955. A canoe was anchored in the middle of Lake Sasajewun, 100 yards from the closest shore and each of us swept for flies with a 1 ft. diameter insect net for a 20 min. period three times a day (7:30 a.m., 1:30 p.m. and 7:30 p.m. approximately) at three to four day intervals. Females of *S. euryadminiculum* were netted in mid-lake sweeps until June 28, but were most numerous in late May and the first two weeks in June as judged by both standard and early non-standard collections (Table I). Three females of *Simulium* (*Eusimulium*) *croxtoni* Nicholson and Mickel were taken in mid-lake sweeps from June 4 to June 17 (Table II).

In the mornings and afternoons few of these flies flew more than 3 in. above the water surface unless disturbed, and most were less than 1 in. above the surface. Occasionally a fly flew just over the canoe (1½ ft.). The flies often flew at great speed past the canoe, but sometimes circled briefly, frequently with their feet dragging lightly on the water surface forming two little trails of ripples. Often the flies touched the water surface and skipped off as if they were ovipositing. On most evenings, however, the majority approached from high level, usually in a spiral, some again flying at high speed. Sometimes they hovered close to our faces occasionally bumping into us, but seldom landing. When disturbed they darted off in a steep upward flight, occasionally horizontally but seldom downward. Flies that were netted had immature eggs and no blood in their ventriculi. Their oesophageal diverticula were full of nectar.

Females of *Simulium* (*Simulium*) *decorum* Walker, *Simulium* (*Neosimulium*) *vittatum* Zetterstedt and *S. venustum* were netted from the canoe from June 7 to July 16 (Table II), but they were much less numerous than *S. euryadminiculum*. Females of *S. venustum* and perhaps others often followed us from shore.

By comparing the species proportion of flies netted in 1955 in different habitats over or near Lake Sasajewun and its outlet, the North Madawaska River, a trend in the abundance of certain species is apparent (Table II). As we go from 100 yards out in the lake to within 8 yards of the shore, to the lake shore itself, to the rapids of the stream 600–1200 ft. below the lake and finally to open areas such as roadways 20–50 ft. away from the stream, there is a continual decrease in the proportion of *S. euryadminiculum* females in the collections and a continual increase in that of *S. venustum* females. *Simulium* (*Eusimulium*) *latipes* Meigen was not taken over the lake and *Simulium* (*Simulium*) *rugglesi* Nicholson and Mickel was taken only over the shore of the lake. However, *S. rugglesi* was netted on June 15 over the water just above the lip of Marsh's Falls (Davies and Peterson 1956). The tendency of *S. croxtoni*, *S. euryadminiculum* and *S. rugglesi* to concentrate near or over water and that of *S. latipes* to be more generally distributed confirms previous observations of Davies and Peterson (1956).

In 1956, one of us (D. M. D.) made collections in the center of Lake Sasajewun. Between 6:30–7:30 p.m. on June 21, 12 females of *S. euryadminiculum*, 3 of *S. croxtoni*, 20 of *S. venustum* and for the first time 3 of *Simulium* (*Eusimulium*) *latipes* (Meigen) or *Simulium* (*Eusimulium*) *gouldingi* Stone were netted. The chances of the last species being *S. gouldingi* are greater in 1956 than in 1955 because more pupae

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[4]Identification was aided by an unpublished key of Shewell (1955), but identification of females of subgenus *Eusimulium* unassociated with their exuviae is only tentative, *S. aureum* excepted.

TABLE I

SEASONAL AND DIURNAL CHANGE IN THE NUMBER OF *Simulium euryadminiculum* NETTED OVER LAKE SASAJEWUN, ALGONQUIN PARK IN 1955 (TWO MEN IN A CANOE EACH SWEPT WITH A 1 FT. DIAMETER NET FOR 20 MIN.)

DATE	TIME			
	7:30 a.m. (7:30 a.m.–8:30 a.m.)	1:30 p.m. 1:30 p.m.–2:40 p.m.	7:30 p.m. (7:20 p.m.–8:05 p.m.)	TOTAL NETTED OVER LAKE
May 27	8[a]	—	—	8
June 4	—	—	24[a,b] x 10+	240–300
June 7	5	44	199[d]	248
June 11	6	1	5	12
June 14	0[c]	1	104	105
June 17	1	0	50	51
June 26	0	0	6	6
June 28	0	0	4	4
July 2	0	0	0	0
July 4	0	0	0	0
July 12	0	0	0	0
July 16	0	0	0	0
July 19	0	0	0	0
July 22	0	0	0	0
Total June 7–June 28	12	46	368	426

[a]non-standard
[b]6:00 p.m.
[c]9:45 a.m.
[d]average of two collections (65 and 333)

TABLE II

A COMPARISON OF THE NUMBER OF FEMALES OF EACH SPECIES NETTED OVER THE LAKE, OVER THE STREAM AND OVER THE LAND DURING THE SPRING AND SUMMER OF 1955. OVER THE LAKE TWO MEN SWEPT WITH INSECT NETS FOR 20 MINUTES. OTHER COLLECTIONS WERE MADE TWO MINUTES AFTER ARRIVAL, ONE MAN MAKING 40 SWEEPS OF THE NET

SPECIES	OVER LAKE		ON LAKE SHORE	OVER RAPIDS IN STREAM	OVER LAND 20–50 FT. FROM WATER
	Mid Lake	Near Shore			
P. decemarticulatum Tw.	0	0	0	0	1
P. hirtipes (Fries)	0	0	0	9	47
C. mulata (Malloch)	0	0	1	0	4
C. subexcisa (Edwards)	0	5	0	0	0
S. (E.) aureum Fries	0	0	2	3[a]	3[a]
S. (E.) croxtoni N. and M.	3	6	3	3	0
S. (E.) euryadminiculum Dav.	657	405	23	12	2
S. (E.) latipes Meigen (or *S. (E.) gouldingi* Stone)	0	0	2	5	2
S. (N.) vittatum Zett.	9	4	1	40	12
S. (S.) decorum Walker	35	36	4	46	23
S. (S.) parnassum Malloch	0	0	1	0	0
S. (S.) rugglesi N. and M.	0	0	7	0	0
S. (S.) tuberosum Lund.	1	0	0	1	0
S. (S.) venustum Say	37	526	157	79[a]	1648
First collection date	May 27	June 7	May 24	May 22	May 21
Last collection date	July 22	July 16	Aug. 6	Aug. 7	Aug. 1
Last flies collected	July 16	July 16	July 18	Aug. 1	July 15
% of *S. euryadminiculum* in total	88	41	12	6	0.1
% of *S. venustum* in total	5	54	79	42	94

[a]One fly netted on September 4 after a gap of one month in collecting.

of this species were found in a stream draining into the lake in 1956 than in 1955. From 7:15–7:45 p.m. on August 4 only 2 females of *S. **euryadminiculum*** were netted over the lake and from 7:30–7:45 p.m. on August 5, 3 females of this species, 2 of *S. **villatum*** and for the first time 1 female of *Simulium* (*Eusimulium*) ***aureum*** Fries. The late, cool spring and summer of 1956 may account in part for the appearance of females of the subgenus ***Eusimulium*** at a later date over the lake in 1956 than in 1955.

In Utah during July 1956, one of us (B. V. P.) noted this "lake-flying" activity twice (limited by the number of collecting trips) for a few females of *Simulium **hunteri*** Malloch and *S. **rugglesi*** over Trial Lake (elev. approx. 10,000 ft.), Uintah Mts. Both species breed in small, rocky streams flowing into the lake.

Two tentative explanations are here proposed to explain the reason for females of *S. **euryadminiculum***, *S. **croxtoni*** and other species flying over lakes. One is that the females were in a pre-mating flight, the males possibly flying higher and orienting themselves near the tops of spruce and other trees near the shore. The other is that the females were flying in search of a blood meal from a water-bird or shore-bird. Preliminary observations suggest that *S. **euryadminiculum***, *S. **croxtoni*** and *S. **rugglesi*** attack ducks only near the water (Fallis, Anderson and Bennett 1956, personal communication). Further careful observations are necessary before a true understanding of the behaviour of these bird-feeding black flies is reached.

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THE STERNAL SCENT GLAND OF EURYCOTIS FLORIDANA (BLATTARIA: BLATTIDAE)[1]

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The cockroach *Eurycotis floridana* (Walker) secretes 2-hexenal in a large median ventral gland in the abdomen (Roth *et al.*, 1956). The gland is a lobed sac formed by an invagination of the epidermis between the sixth and seventh abdominal sternites. Two distinctly separated lobes of the gland arise on each side of the ventral nerve cord and extend forward to the third sternite (fig. 1). The large lobes consist of two or three less distinct lobes. When the gland is distended with fluid, its surface is smooth and the lobes are distinct. Tracheae, branching from the median ventral tracheal trunks, ramify extensively over the surface of the gland. Fat body is closely associated with the scent gland by means of tracheal attachments. Inconspicuous longitudinal muscles arise along the ventral surface of the two main lobes and insert near the median line at the anterior edge of the sixth sternite. No detectable nerves are connected with the gland. The gland opens to the exterior between the sixth and seventh sternites. A U-shaped indentation in the middle of the anterior margin of the seventh sternite delimits the dorsal side of the opening; the ventral side of the opening is slightly wider (fig. 2). Just posterior to the aperture of the gland is a crescent-shaped, rigid thickening in the intersegmental membrane (fig. 2,R). As there is no sphincter muscle at the opening of the gland and no muscles in the wall of the sac, the discharge of fluid from the gland seems to be controlled by the longitudinal muscles which attach the gland to the sixth sternite. Contraction of these muscles would elongate the sac and thereby decrease its volume and force the fluid out through the narrow slit of the closely opposed sternites (fig. 3). Similarly, general contraction of the abdomen would compress the fluid-filled sac and force out the liquid. The fluid can be ejected for a considerable distance (Roth *et al.*, 1956).

The scent gland is present and functional in adult males and females. If the cockroach is immobilized by cooling to 4°C, the sac can be dissected without having the fluid ejected. At emergence of the adult, no 2-hexenal could be seen in the scent gland but, when opened, the sac smelled faintly of the aldehyde. One day after emergence, small globules of secretion were visible; at four days, slightly larger globules had

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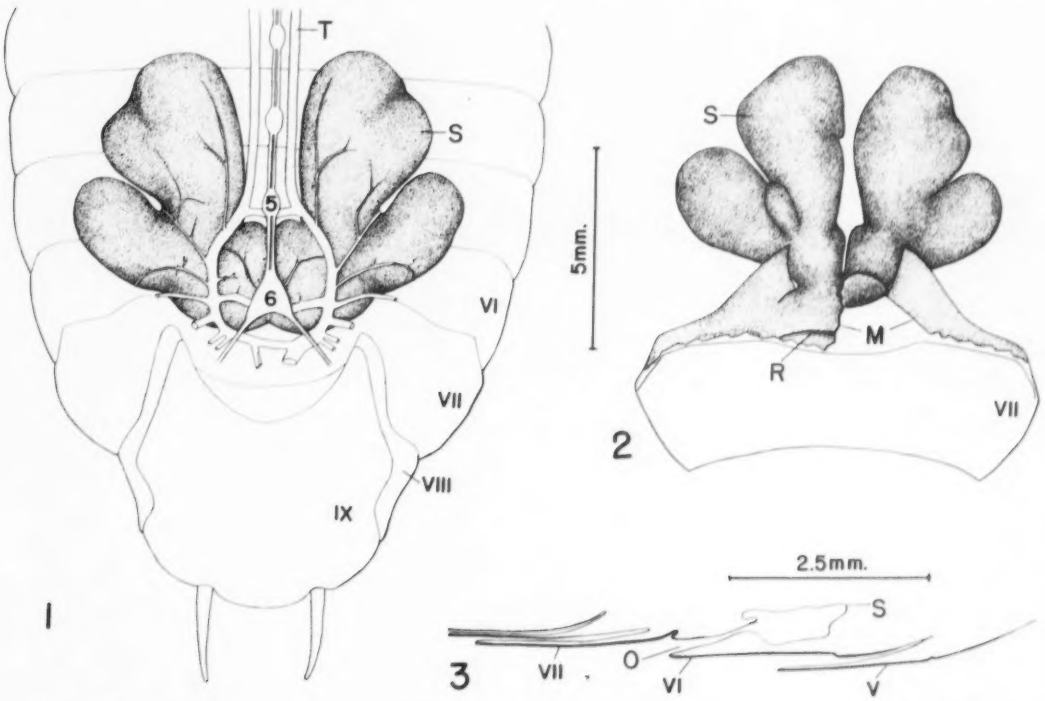
been formed. By nine days after emergence, the lobes of the gland were distended with large globules of secretion. In still older roaches, the gland was completely distended with secretion.

Scent glands were fixed in alcoholic Bouin's fluid, 80% alcohol, Helley's and Zenker's fluids. Sections, 5 μ thick, were stained with Delafield's hematoxylin, Mallory's triple stain, periodic acid Schiff (PAS) reagent (Lillie, 1948) and Gomori's (1952) alkaline phosphatase stain.

The wall of the sac is composed of an outer cuticular membrane, two cellular layers and an inner cuticular lining which is continous with the cuticle (fig. 4). Tall columnar secretory cells form the outer cellular layer, whereas the inner layer is formed of small squamous cells. The layer of secretory cells is discontinuous, so that between the clusters of secretory cells the wall of the sac is thin (fig. 4).

The secretory cell is characterized by a large, oval, basal nucleus, granular cytoplasm, and a cylindrical secretory apparatus. Within the striated secretory apparatus arises a cuticular tubule which extends up through the cell and along the surface of other cells (figs. 5, 6). In certain areas numerous tubules, sometimes as many as 25 or 30, open into the cuticular lining of the sac. Three tubules are shown opening into the lining in figure 10. Tracheoles penetrate between the secretory cells. The nuclei of the inner layer of cells are small but conspicuous (fig. 6); their cytoplasm is extremely thin and almost indistinguishable. Cell division was not observed in the adult gland.

The adult scent gland varied in its reaction to Schiff reagent after periodic acid oxidation. The purple staining material which was removed by pretreatment with saliva was considered to be glycogen. A series of scent glands from adults of various ages was studied in an attempt to coordinate the presence of glycogen with the secretory activity of the cells. Recently emerged adults were isolated and kept undisturbed from one to 33 days. Glycogen was more abundant in the cells of the scent glands of young cockroaches than in those of older insects. The cells of the scent glands of newly emerged cockroaches were laden with glycogen and all of the scent glands from the twelve cockroaches, less than two weeks of age, contained glycogen. On the



FIGS. 1-3. Semidiagramatic drawings of the scent gland of an adult male of *Eurycotis floridana*. 1. Dorsal view of the scent gland showing the position of the gland (S) in relation to the sternites (VI-IX), fifth and sixth ganglia (5, 6) and tracheal trunks (T). 2. Ventral view of scent gland (S) and seventh sternite (VII). The sixth sternite and part of the intersegmental membrane (M) have been cut away. Note the rigid area (R) in the intersegmental membrane. 3. Median longitudinal section through the scent gland (S) and sternites (V-VII) showing the opening (O) of the gland.

other hand, five of the twelve scent glands from cockroaches between 13 and 33 days of age lacked glycogen. A scent gland from a 27-day-old male *Eurycotis* was examined and found to lack any aldehyde odor. This scent gland was also devoid of glycogen. Four 13-day-old adults were made to eject their secretion by anesthetizing them with CO_2. Two days later, the gland sacs contained large globules of 2-hexenal but were not fully distended. The glands were fixed and stained for glycogen. The glands of four 15-day-old adults which had been isolated at emergence and kept undisturbed, were fixed as controls. Scent glands from three of the insects which had discharged the aldehyde two days previously contained considerable glycogen; one completely lacked glycogen. Of the controls, one showed no glycogen, one little glycogen, one a moderate amount, and only one considerable. The glycogen-filled secretory cells of a 7-day-old cockroach are shown in figure 8. Here a glycogen-laden cell is adjacent to one devoid of glycogen; this was a common occurrence. Also, in a single gland one may find groups of cells containing glycogen and groups without glycogen.

In addition to glycogen, other elements of the secretory cells were stained conspicuously with PAS. The tubules within the secretory apparatuses were stained red (figs. 6, 9), and the secretory apparatuses were frequently red but not as dark as the tubules. These elements were stained regardless of the fixatives used. On the other hand, distinct red granules surrounding the secretory apparatuses (fig. 9) were demonstrated after fixing in alcohol or Helley's but not after fixing in alcoholic Bouin's fluid. The presence of glycogen may obscure the granules but they were readily visible in preparations pretreated with saliva. The abundance of granules and glycogen was not always concurrent. Granules might be present in the absence of glycogen. The scent gland was unstained by Schiff reagent alone.

A most outstanding demonstration of the secretory apparatus was produced with Gomori's test for alkaline phosphatase. The area of the secretory apparatus was intensely blackened, whereas the nuclei and cytoplasm were lightly stained (fig. 7). The absence of glycogen in the secretory cells was not noticeably accompanied by a decrease in alkaline phosphatase.

In young nymphs the gland appears first as two tiny pointed sacs. In the last nymphal instar, the sacs are large, rounded and lobed. The muscles which attach the gland to the sixth sternite are more readily observed in the small nymphal gland than in the adult. At the end of the last instar, the gland is fully formed but apparently does not produce the odorous secretion.

Nymphal glands were stained with Mallory's triple stain, Feulgen reagent, PAS, and Gomori's alkaline phosphatase stain. The very small gland was composed of closely packed nuclei. Cell boundaries were indistinguishable. Mitotic figures appeared on the inner surface of the gland wall (fig. 11) and numerous chromatin bodies were discharged into the lumen. After the last nymphal instar had undergone about two-thirds of its development, mitosis ceased, the nuclei appeared in clusters, and cell boundaries were distinguishable in the apical cytoplasm (fig. 12). Figure 13 shows a distinct differentiation of cells in the nymphal gland. The apical cytoplasm of the clustered cells is dense and devoid of glycogen, and apparently pours out secretion. Nymphal glands were distended with viscous material which was preserved in fixation and was stained pink with PAS and blue with Mallory's triple

EXPLANATION OF FIGURES

FIGS. 4–13. Photographs of 5 μ cross-sections of scent glands of the cockroach *Eurycotis floridana* (figures 4 through 10, from adult males; figures 11 through 13, from nymphal males).

FIG. 4. Cross-section of one lobe of the scent gland. The columnar secretory cells occur in clusters, hence the thin areas in the wall of the sac. Note the cuticular lining. Alcoholic Bouin's, Mallory's triple. × 50.

FIG. 5. A portion of the gland cells shown in figure 4. The columnar secretory cells rest on a thin basement membrane and contain conspicuously stained secretory apparatuses. Above the secretory cells are dark nuclei of squamous epithelial cells and the membranous lining. × 880.

FIG. 6. A preparation fixed in alcoholic Bouin's solution stained with periodic acid-Schiff (PAS) reagent and haematoxylin. The secretory apparatus and the tubule within it are stained red but the cytoplasm is not colored. Note the nuclei of the squamous epithelial cells above. × 1590.

FIG. 7. Alkaline phosphatase is demonstrated in the region of the secretory apparatus with Gomori's procedure. × 1120.

FIG. 8. Glycogen is demonstrated with PAS reagent in secretory cells of a scent gland fixed in 80% alcohol. × 1120.

FIG. 9. Secretory apparatuses of the same gland pictured in figure 8. This section was pretreated with saliva and stained with PAS. The masses of glycogen are removed but red granules persist around the secretory apparatuses. Note in figure 6 that no granules are demonstrated with PAS after fixation in alcoholic Bouin's fluid. × 1120.

FIG. 10. Tubules which arise in the secretory apparatuses are shown opening into the cuticular lining. Alcoholic Bouin's, Mallory's triple. × 1880.

FIG. 11. Part of a cross-section of a small nymphal scent gland. Note the numerous small nuclei and mitoses adjacent to the lumen of the sac. Alcoholic Bouin's, Feulgen and light green. × 440.

FIG. 12. Part of a cross-section of a scent gland from an older nymph. No mitosis is visible; differentiation of cells is evident. Alcoholic Bouin's, Feulgen and light green. × 440.

FIG. 13. Nymphal gland similar to that of figure 12. Glycogen is demonstrated around the large nuclei. The clusters of cells with small nuclei are devoid of glycogen but are stained pink after pretreatment with with saliva. Alcoholic Bouin's, PAS. × 1120.

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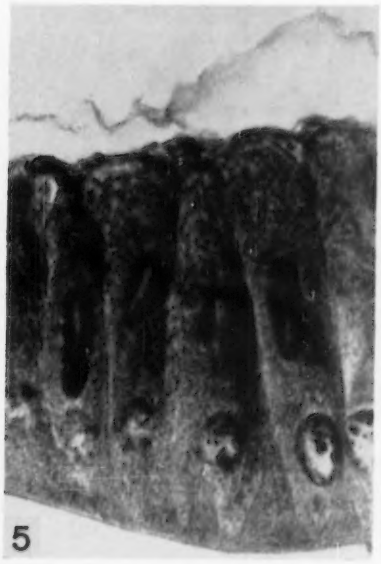
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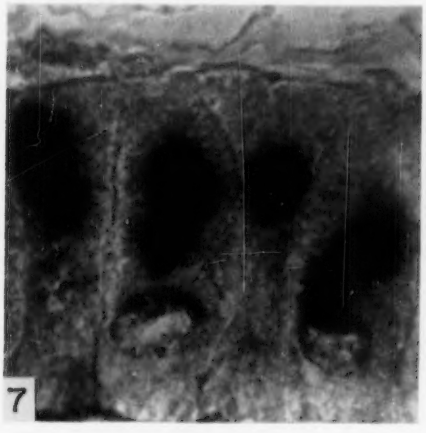
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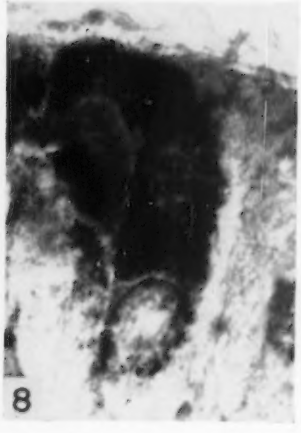
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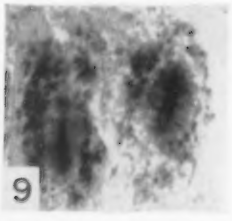
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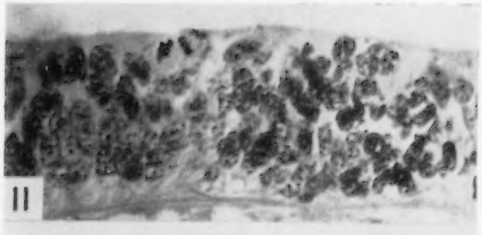
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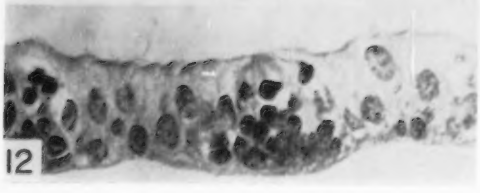
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stain. The cells between these clusters had larger nuclei (figs. 12, 13) and contained deposits of glycogen (fig. 13). During the last third of the final nymphal instar the cells continued to differentiate until, a few days before emergence, the gland appeared much like the double layered gland of the adult. Tall columnar secretory cells formed the outer layer of the gland. The inner layer was composed of small epithelial cells underlying a much-folded cuticular lining. Both cell layers were laden with glycogen. The tubules in the apexes of the secretory cells were stained pink with PAS reagent and, in some nymphs, were surrounded by granules which resisted treatment with saliva. Alkaline phosphatase activity in the region of the secretory apparatus was found only in the differentiated glands of the fully grown nymphs.

DISCUSSION

The morphology of the scent gland of *Eurycotis floridana* is similar to that of the sternal organ of *Blatta orientalis* L. (Harrison, 1906; Stanislavskij, 1926) and the ventral gland of *Periplaneta americana* (L.) (Liang, 1956). Similar glands have also been observed in *Neostylopyga rhombifolia* (Stoll) and *Platyzosteria novaeseelandiae* Brunner (Roth and Willis, unpublished). In size and shape, the gland of *Eurycotis* most closely resembles those of *Neostylopyga* and *Platyzosteria*. The gland of the oriental cockroach is less lobed and much smaller in proportion to the size of the insect.

The cellular structure of the gland of *Eurycotis* appears to be similar to that of *B. orientalis*. However, Harrison did not observe the continuity of the intracellular tubules of the gland cells with the tubules which join the lining membrane. She considered the inner layer of irregular nuclei to be degenerating gland cells which had migrated inwards. It seems unlikely that the gland cells degenerate, for no regenerative cells or mitotic figures have been observed in the adult gland cells, and the secretory cells do not appear in various stages of degeneration. It seems more likely that the inner layer of nuclei are comparable to the "chitinogenic" layer of cells (Konček, 1924) or "supporting cells" (Oettinger, 1906) described in the tergal glands of *Blattella germanica*. Konček believed these small cells were responsible for the formation of the secretory ducts as well as the chitinous covering. Stanislavskij (1926) recognized the similarity in structure between the sternal scent gland and other hypodermal glands of the oriental cockroach.

Although Roth (1952) failed to observe tubules in the cells of the tergal gland of males of *Supella supellectilium* (Serv.) a reexamination of his original slides shows that the cells are similar to those of tergal glands of males of other species of cockroaches. The secretory cells possess secretory apparatuses and tubules, and lie under a layer of small "chitinogenic" cells. The colleterial glands of the female *Periplaneta americana* (Linn.) (Brunet, 1951) and the male accessory glands of *Leucophaea maderae* (Fab.) (van Wyk, 1952) are examples of glands which have structures basically similar to the ventral scent gland and the various tergal glands already described.

There was no change in the size of the secretory cells or in the condition of their cytoplasm or nuclei which would indicate a drastic change in the physiological activity of the secretory cells. Only changes in the occurrence of glycogen and PAS-positive granules suggest a cyclic activity. From the brief survey of the occurrence of glycogen in the secretory cells, it is not possible to establish definitely a secretory pattern of the scent gland. However, if the presence of glycogen is an indication of secretory activity of the cells, it would appear that the scent gland pours out secretion until the sac is fully distended, tapers off secretion until the fluid is discharged, and then actively secretes again. The secretory activity of the cells is probably not synchronous, inasmuch as glycogen may be absent and present in adjacent cells.

The manner in which glycogen may be linked to the production of 2-hexenal is a matter for further biochemical investigation. The granules around the secretory apparatuses and the material within the secretory tubules, demonstrated by Schiff's reagent after periodic acid oxidation, are probably more closely related to the aldehyde. The secretory granules and the material within the tubules apparently differ in composition, for the tubular material stains after fixation in either alcoholic Bouin's fluid or alcohol, while the granules are not preserved with alcoholic Bouin's fluid.

The author gratefully acknowledges the interest and critical advice of Louis M. Roth and thanks E. R. Willis for reading the manuscript critically.

SUMMARY

1. The morphology of the sternal scent gland which secretes 2-hexenal in *Eurycotis floridana* is described.

2. Histologically, the gland consists of an outer layer of tall, columnar, epithelial cells, an inner layer of small, squamous, epithelial cells, and a cuticular lining. The secretory cells are characterized by secretory apparatuses and minute tubules which convey the secretion to the lumen of the sac.

3. Histochemical tests revealed the presence of glycogen and other periodic acid Schiff-positive material in the secretory cells and a high level of alkaline phosphatase activity in the regions of the secretory apparatuses.

4. The nymphal scent gland, though well developed in the last instar, does not secrete 2-hexenal. The development of the nymphal gland is described briefly.

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THE DIVERTICULUM OF STILBOMETOPA IMPRESSA (BIGOT) AS A FUNCTIONING ORGAN (DIPTERA: HIPPOBOSCIDAE)[1]

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INTRODUCTION

There has been a great deal of conjecture concerning the function of the diverticulum in the obligatory ectoparasites of birds and mammals belonging to the family Hippoboscidae. Bequaert (1953) states that Dufour (1845) overlooked the organ in *Melophagus*, *Hibbobosca* and *Ornithomyia*, and that Roubaud (1909) also failed to mention its existence in *Melophagus*. The presence of a diverticulum in the Hippoboscidae was first recognized by Massonnat (1909) who pointed out that the organ was more fully developed in avian than in mammalian species. He further stated that he often saw blood corpuscles in the diverticulum of *Pseudolynchia*. Massonnat's findings were confirmed by Hoare (1923) for *M. ovinus* (Linnaeus); Theodor (1928) for *Lipoptena capreoli* Rondani, *H. camelina* Leach and *H. equina* Linnaeus; and Adie (1915) for *P. canariensis* (Macquart). However, these workers did not find blood *per se* in the diverticula of the species of flies they worked with. Theodor noted that the diverticulum of *L. capreoli* also sometimes was filled with a yellowish fluid.

During the author's investigations of the biology of *Stilbometopa impressa* (Bigot), a hippoboscid found on the California quail *Lophortyx californica californica* (Shaw and Nodder) (Tarshis, 1953), special attention was focused on the question of whether the diverticulum of this species was a functioning organ or not. This question was subsequently answered affirmatively and data collected during this study on the diverticulum of this species of Hippoboscidae are presented herewith.

EXPERIMENTAL DATA

In *Stilbometopa impressa* the rather large, bilobed portion of the diverticulum is found in the upper two-thirds of the abdomen, in front of the excretory glands of the salivary system (ventral view). Details on the entire salivary and digestive systems of this species and the dissection technique used in studying them are to be found in previous papers (Tarshis, 1953, 1955). The bilobed portion of the diverticulum opens off a very small tube that branches off the cesophagus. It has been found to be extremely dilated and to have very smooth, elastic outer walls and an interior filled with a lacy network of fine, anastomosing fibers which form innumerable, irregularly shaped small spaces.

In newly-emerged flies the diverticulum generally looks like an inflated balloon and in most cases is devoid of a cleft. The walls seem to be tougher and more elastic at this stage than at any other and when one attempts to puncture the empty organ with a dissecting needle the needle bounces off the walls rather than piercing them. One to several bubbles are most generally found in the diverticulum of newly-emerged flies and, though they vary in size, they are always found just below the neck of the diverticulum (fig. 1).

Though in the majority of instances the diverticula present more or less uniform appearances at the same stages of feeding, there are variations and deviations in size and shape.

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Diverticula have been observed completely devoid of blood, partially filled, completely filled and with only traces of blood left in the crevices of some of the irregularly shaped inner spaces of the lining (fig. 1).

After dissecting and observing diverticula in more than 300 fed specimens of *S. impressa* the writer has concluded that the appearance and function of the diverticulum during feeding by both male and female flies generally follows the pattern detailed in fig. 2.

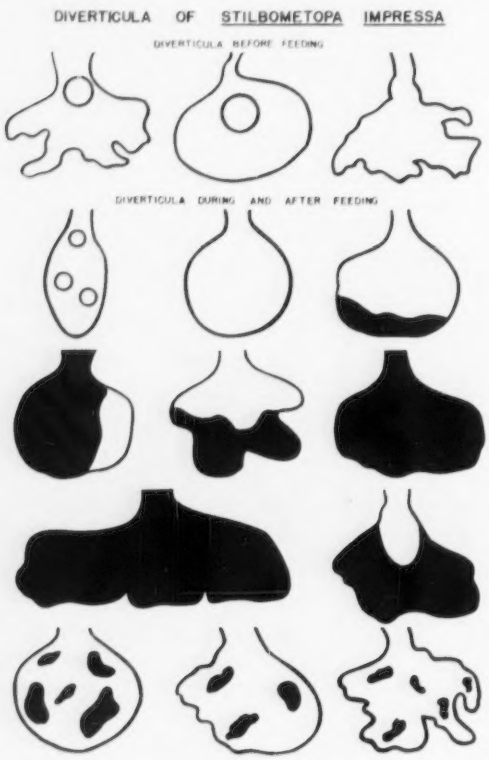

FIG. 1.—Diverticula of *Stilbometopa impressa* (Bigot) before and after feeding.

Stilbometopa impressa of both sexes feed about once every six days; the frequency of feeding by this species seems to be primarily determined by the blood capacity of the diverticulum and gut, and by the amount of blood utilized each day from the stored blood supply in the diverticulum. The frequency of feeding by the females seems to be correlated with their six-day gestation period (Tarshis, 1957), but, since males of the species feed as infrequently as females, gestation is apparently not the sole determining factor in the frequency of feeding.

Female flies, returning to quail after leaving the birds to deposit their prepuparia, commence to feed as soon as they become re-established on the quail. The re-establishment may take from a few minutes to several hours. Once feeding commences the flies do not stop until their guts and diverticula are filled to capacity.

Dissections made on gravid females show that during the first two days of gestation all the blood in the gut and about one half of the blood in the right lobe of the diverticulum is fully

FIG. 2. Steps in the utilization of the blood in the diverticulum of *Stilbometopa impressa* (Bigot). A. During the primary stages of feeding the fly fills the entire gut, then it commences to fill the diverticulum, which is still inflated, but is devoid of a bubble and has a cleft. B. After blood has filled the diverticular tube it begins to flow simultaneously into both lobes of the diverticulum. C. Blood continues to fill the diverticulum until the entire organ is completely filled and expanded with the blood. Sometimes the cleft between the lobes is completely obliterated, or the shape is altered as shown here. D. Once the gut and diverticulum are filled with blood, the fly apparently ceases to feed until the blood supply in both organs is completely exhausted. It seems that the blood in the gut is digested first, then little by little, the blood in the right lobe of the diverticulum is utilized. E. As the blood in the right lobe of the diverticulum is withdrawn, the lobe becomes deflated and wrinkled, and the blood is drawn a little at a time from the left lobe. F. When the blood supply in both lobes of the diverticulum has been completely exhausted, the organ is deflated, limp, and wrinkled with only small scattered blotches of blood remaining in the crevices of the small inner spaces of the lining.

digested. After the larva has undergone four days of development the fly has utilized all the blood stored in the remaining half of the right lobe of the diverticulum and part of the blood in the left lobe. By the time the prepuparium is deposited on the sixth day of gestation only traces of blood are left in the diverticulum. This diminution of the blood supply during the development of the larva is understandable, since, as the larva develops it swells the abdomen and pushes the diverticulum and mid-gut and part of the hind-gut upwards towards the waist of the fly. It would be quite impossible for the fly to carry simultaneously a larva and the large quantity of blood that she ingests after each blood meal.

Male *S. impressa* placed on quail at the same time as gravid females and dissected after the same time intervals have been found to utilize the blood in the gut and diverticulum in about the same time and manner as the females.

SUMMARY

The diverticulum of *Stilbometopa impressa* (Bigot) has been found to be a functional organ. Both sexes of *S. impressa* feed once every six days until the gut and diverticulum are filled to capacity, then derive all nourishment for the next six days from the stored blood supply in the gut and diverticulum.

ACKNOWLEDGEMENTS

The author wishes to express sincere appreciation to Dr. M. A. Stewart, Professor of Parasitology, University of California, under whose supervision this work was done and to Dr. J. Bequaert, formerly of the Museum of Comparative Zoology at Harvard College for his enthusiastic encouragement and help.

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THE WATER RELATIONS OF TERRESTRIAL ARTHROPODS, by E. B. Edney. Cambridge Monographs in Experimental Biology, No. 5, Cambridge University Press, New York. vi+109 pp. 32 figs. 1957. $3.00.

Intimately concerned with life on land are the modifications for getting water and more particularly for not losing excessive amounts of it. The various facets of this problem form the subject of this pocket-size monograph in which the method of presentation is kept simple so that it is readily understood by the general entomologist and general biologist. It could be assigned as reading in undergraduate courses after a first college course in elementary zoology or elementary biology. It does not seem appropriate however for the amateur or lay reader.

After a short introduction treating the physics of evaporation, separate chapters are devoted to the structure of the cuticle in relation to transpiration (water loss by evaporation), excretion and osmoregulation in general, the gain in water by various means, and the relation between water and body temperature. A final chapter collates these into a set of general conclusions with emphasis on what is still uncertain or unproven. The bibliography of about 250 references includes full titles.

Although the title, and main discussion, is limited to terrestrial species, mention is occasionally made to aquatic forms for comparative illustrations to illuminate certain points. Despite this, treatment of crustacea is limited to the isopods with no mention of the decapods, some of which are well-known to invade the land habitat for significant periods of time. Of course, the decision to include or exclude such forms is arbitrary, and, indeed, the author's first sentence states that the scope must be arbitrarily delimited. However, both for feeding and for migration a number of decapods do come onto land, even into dry surroundings.

In general, the various chapters are divided into sections treating the phenomena involved. Thus in the chapter entitled "Gain of Water," he treats successively: intake with food, oral and anal drinking, absorption of fluid water through the cuticle, metabolic water, absorption of water vapor including discussion of the difficult problem of explaning this surprizing phenomenon, and finally absorption of water by eggs. In some cases the material is presented historically with a listing of the hypotheses that have been suggested (a feature this reviewer commends).

Somehow I did not find this book fascinating to the extent of, for instance, Krogh's little book on osmoregulation published almost 20 years ago. Nonetheless, Dr. Edney has brought together a large part of the relevant literature, and has mostly treated it in an objectively critical manner. Accordingly the volume will be of considerable use, especially to ecologists who will find it convenient to have these data readily available in convenient form.

A. Glenn Richards.

BIOLOGICAL OBSERVATIONS ON EXOMALOPSIS (ANTHOPHORULA) CHIONURA COCKERELL, INCLUDING A COMPARISON OF THE BIOLOGY OF EXOMALOPSIS WITH THAT OF OTHER ANTHOPHORID GROUPS (HYMENOPTERA: APOIDEA)

JEROME G. ROZEN, JR.[1,2] AND C. DON MACNEILL[2]

Although it is always of value to add hitherto unknown information to the fund of knowledge concerning the habits and life histories of the Apoidea, the data presented below are of special interest because they help to demonstrate the relationship of *Exomalopsis* and the Exomalopsinae with certain other groups of the Anthophoridae. This relationship has been a moot question in the phylogenetic understanding of the bees, as discussed by Michener (1953). The information supplements that set forth in another paper (Rozen, 1957) and corroborates the conclusions therein.

Specimens of the cocoons and larvae as well as a number of plastercasts of the burrows have been deposited in the collection of the California Insect Survey, University of California, Berkeley.

DESCRIPTION OF LOCALITY

E. chionura was discovered nesting by William Kellen at Alpine Lake, Marin County, California. During the period of adult activity, the authors visited the site four times, August 4, 12, and 20, and September 1, 1955. All were warm clear days, except the last which, though the warmest, was partly cloudy.

The nesting site was situated in a small, shallow, south-facing valley which descends at a 15 to 20 degree angle from a hilltop approximately one hundred yards distant. A few yards below the site, the slope steepens and extends five hundred yards to the shore of Alpine Lake. Grasses and low herbage intermixed with clumps of chaparral comprise the vegetation over most of the hill including the valley. Here and there, particularly along the rim of the valley, weathering rock outcroppings of a serpentine nature protrude and unquestionably account for many of the small rocks scattered over the valley. Because of the influence of water on soil fissures, it is significant to note that rains are seasonal in this region, being restricted to late fall, winter, and early spring.

The site itself occupied an area approximately 12 by 14 feet in the middle of this valley and bore no physical characteristics which distinguished it other than the multitide of bees which zigzagged over it. It is interesting to note that, when Kellen discovered the site, he was first attracted to it by the humming produced by the bees (noticed by us only on calm days). The authors estimated between five hundred and a thousand individuals were flying at one time over the nesting area, most of them being concentrated in an area of only 6 to 8 feet in diameter.

The vegetation type at the nesting site was dominantly grass (several species), though dicotyledonous plants including a yellow composite and *Lessingia ramulosa* var. *micradenia* (Greene) J. T. Howell, also a composite, were present. The grass grew primarily in clumps, between which occurred exposed areas of ground and less prominent plants. No chaparral approached close enough to shade the site any time during the day. While one of the pollen plants, *L. ramulosa* var. *micradenia*, existed both on and next to the site, a somewhat denser stand grew 20 feet away.

The exposed surfaces consisted of loose or partly consolidated soil, approximately one-half centimeter thick, which contained small pebbles and some dried plant stems and leaves. Also scattered about were several rather large decomposing rocks.

Numerous, rather sinuous cracks extended across the site and were also present elsewhere in the valley. Some were quite long (perhaps 6 feet) and wide (up to 2 cm.) though the apposed surfaces were irregular. However, these fissures usually appeared shorter and narrower because of sections being hidden or partly obscured by vegetation or the surface layer of soil. Traversing in various directions, they seemed to have no particular orientation, were often interconnected, and at least one is known to have penetrated appreciably below 55 cm. Judging from the cracked appearance of lumps of soil allowed to dry in the laboratory, it is obvious that these

[1]The research was undertaken and the manuscript prepared while this author was associated with the California Insect Survey, University of California, Berkeley. His address is now Entomology Research Branch, U. S. Department of Agriculture, Washington 25, D. C.

[2]We would like to express our appreciation to Professors E. Gorton Linsley and J. W. MacSwain, of the Department of Entomology and Parasitology, University of California, Berkeley, for reading the manuscript and suggesting a number of helpful improvements. They also generously permitted us to study several of their papers which had not yet been published and also to examine specimens upon which their work in part had been based. These acts have enabled us to make a much more accurate comparison of the biology of *Exomalopsis* with that of other groups than would have been possible otherwise. Accepted for publication March 11, 1957.

crevices resulted from the gradual desiccation of the ground during the dry season. An examination of the site after commencement of fall rains revealed that they had closed. It is obvious that cracking may occur at different places each year, because many old bee cells were exposed along the faces of the fissures.

The soil of the site was heavy and clay-like throughout, and, where excavated, contained small stones as well as several large ones. It was visibly stratified into two major layers, in addition to the thin loose surface stratum mentioned above. The upper, approximately 12 cm. in thickness, was light-colored, without visible signs of moisture, and extremely hard, necessitating the use of a small pick ax for digging. A darker moist layer of the same clay-like material lay beneath and though compact could be excavated more easily. In the latter, the cells of *Exomalopsis chionura* were discovered.

NESTING ACTIVITY

The cracks in the soil played an important role in the nesting activity of these bees, for it was by descending through them that the females gained entrance to their burrows; no burrow openings were found on the surface. Usually many bees were noticed disappearing through a relatively short length of crack, apparently because the fissure was obscured elsewhere by surface soil and debris. One was so completely covered that only a small burrow-like opening remained, through which several females entered the ground. Although we first believed it was an exposed burrow opening, the fissure was revealed when the soil and debris were removed.

Through the excavation of all the earth on one side of a crevice, a number of circular openings were discovered on the exposed vertical face in the vicinity of the 45 cm. level. These measured 2 mm. in diameter and a few may have possessed a small amount of excavated soil plastered around the lip. While some may have represented emergence holes of adults, others were certainly burrow entrances, as was evidenced by the considerable accumulation of excavated soil below in the crack. The tunnel leading from the crevice descended initially at approximately a 45 degree angle. For reasons presented below it appears, however, that the general direction of the burrow is horizontal.

The soil which had been removed through the digging of the tunnel was moderately fine, loose, and very even-grained. Hence, it is easily distinguished from surface soil which may fall by chance into the crevice. At the bottom of one large fissure, the excavated material was copious and could be measured in terms of tablespoonfuls.

Partly because of the nature of this material, it can be concluded that the bees do not employ water in digging as do some of the emphorines (Linsley, MacSwain, and Smith (1956) state that the emphorines manufacture mud pellets from excavated soil). Furthermore, there would seem to be no need for water since *E. chionura* gains access to moist, easily dug soil by descending into the cracks.

There is a possibility that more than one female uses a single nest entrance. This is indicated by the fact that relatively very few burrow openings were encountered in proportion to the many existing cells.

The configuration of the nest of *E. chionura* was not completely worked out. Not only did insufficient time prevent this but the soil of the nesting site was riddled with a multitude of burrows and hundreds of cells (from present and past generations), creating considerable difficulty in tracing even a short section of a tunnel. In regard to the main tunnel, its diameter is known to be approximately 2.5 mm. and its direction variable, for the same tunnel may ascend, then descend, turn either to the left or right. Furthermore, the burrow forks a number of times. One particular section (7 cm. in length) that could be easily studied exhibited six dichotomies.

An examination of the surface of the burrow revealed that much, and perhaps most, of it has been lined with soil. This built-in wall is variable in thickness, though usually thin, and almost always rough, unlike the cell wall. Septa of the same rough appearance are occasionally encountered, blocking off sections of tunnels or whole branches. Their function is discussed in the following paragraph. In places there is no indication of a lining having been applied to the tunnel, in which case the wall is incised by elongate, usually somewhat diagonal indentations, presumably caused by the mandibles of the female.

A tunnel may be used during more than one season, as is evidenced by cells of the present and past generations opening into it. In one easily traced section of a burrow it was noticed that septa barred the way to old cells, perhaps indicating that all extraneous passageways may be so blocked by the female. Furthermore, it may suggest that the constructed walls of the tunnel and cells are an expression of a broader innate behavior pattern, *viz.*, to fill in areas which do not conform to the "proper"dimensions.

Many hundreds of cells were encountered during the course of the excavation of the site. Almost all were uncovered below the 25 cm. level (well beneath the upper dry layer of earth) and occurred to a depth of approximately 50 cm. In general they were concentrated about the middle of the lower 25 cm. stratum. In view of the depth (approximately 45 cm.) of the burrow openings, it must be concluded that the tunnels are horizontal in general direction even though tortuous in path.

Internally the cells are elongate spheroids, approximately 6.0 mm. (five data) in length with

a circular cross-section of approximately 3.6 mm. (seven data) in diameter. Although their long axis may be horizontal to vertical, most were inclined at an intermediate angle. The anterior end (mouth) was never the lower. Cells may be arranged singly or in a linear series. As many as five cells have been found so connected, though even longer sequences may exist. Although a series may form a straight line, more often it is curved. It was noticed that the length of the tunnel connecting the cells was at least usually somewhat shorter than that of a cell and was filled with a fairly hard soil.

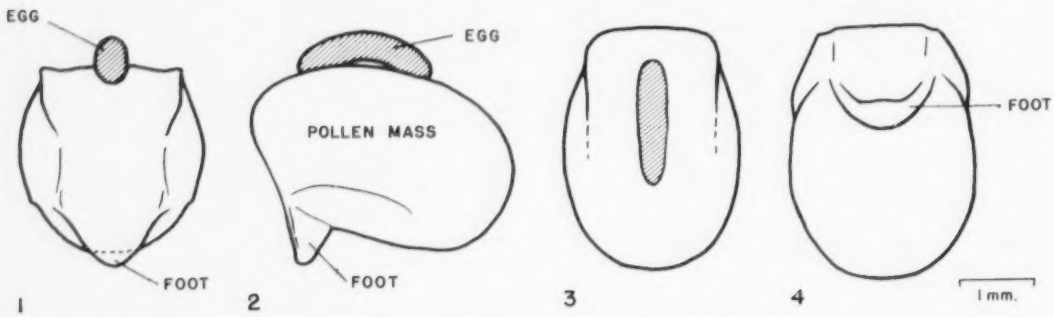
From an examination of occupied, and hence recently constructed cells, it is obvious that a bee first excavates a concavity and then builds a wall into it with the even-grained excavated soil. Apparently because of the irregularities in the concavity, the wall varies in thickness from place to place and may even be partly absent. In one particular cell, the thickness ranged from 1.5 mm. to less than 0.25 mm. With cells remaining from previous years, the wall is altered so as to become nearly indistinguishable from the surrounding soil. The cell wall cannot be removed intact as in *Anthophora* and the emphorines.

The inner surface of a cell appears smooth and has applied to it a conspicuous shiny wax-like coating, which is non-permeable to droplets of water placed upon it.

The female carries pollen in a dry state into the completed cell. She moistens and shapes it into an elongate, somewhat angulate form (figs. 1–4), which bears the approximate dimensions: length 3.5 mm. (five data); width 2.2 mm. (three data); and breadth 2.4 mm. (four data). Although not noted for cells oriented vertically, the mass is so situated that its rounded posterior end adjoins that of the cell. Furthermore, it can be seen in freshly unearthed cells that an abundance of liquid is present at this junction and thus seems to serve as an adhesive to hold the surfaces together. Other than this connection, no part of the food contacts the cell wall except a ventral foot-like projection, the anterior surface of which is continuous with that of the pollen mass.

At least in cells which are horizontal or partly inclined, the elongate, cylindrical, translucent whitish, somewhat curved egg is deposited on top of the provisions. Its chorion is completely smooth, bearing no reticulations. The egg is situated on the median line of the pollen mass, somewhat forward of center, with its long axis parallel to that of the food. Its anterior end usually, and perhaps always, faces the cell mouth, and, because of its curvature, only the anterior and posterior surfaces probably ever contact the pollen. In length the newly deposited egg measures approximately 1.7 mm. and the diameter at the widest point is 0.4 mm. (figures based upon two eggs).

The cell is then closed with a spiral plug composed of excavated soil, which is hardened, presumably by some secretion applied by the female.



Egg and pollen mass of *Exomalopsis chionura* Cockerell.
Fig. 1. Anterior view. Fig. 2. Lateral view. Fig. 3. Dorsal view. Fig. 4. Ventral view.

DEVELOPMENT

Because the prehibernating larvae are very delicate, apparently succumbing to heat, only a few have been successfully transported to the laboratory, where their development and behavior could be studied. All of these were mature or nearly mature forms. However, some information concerning earlier stages can be deduced from other evidence on hand.

During the period of feeding, the larva moves circularly about the pollen mass. This is indicated not only by the various positions in which the individuals were found when excavated but also by the presence of channels incised in the provisions as the larvae move about. The impressions become wider as the larva increases in size. Similar grooves have been reported for some of the emphorine genera with this habit (Linsley, MacSwain and Smith, 1956). As with

these other genera, the larva of *E. chionura* is elongate and possesses a protruding ninth abdominal sternum. Linsley, *et al.*, (*ibid.*) have pointed out that these modifications probably represent adaptations for the ambulations.

Because the place of deposition of the feces is determined in part by whether or not a cocoon is eventually spun, it is necessary to consider the frequency of cocoon making before discussing the matter of defecation. In the majority of cases, the larva spins a cocoon which is composed of fecal material incorporated into strand upon strand of matted silk, as is described below. Not infrequently, however, a cocoon is encountered which possesses either but a small quantity of excrement or sometimes also only a small amount of silk. A sufficient number of these "abnormal" ones have been seen to strongly indicate through their variability that they are intermediate between the fully developed cocoon and the cocoonless condition. This last state, though representing only a fraction of the population, is known in some twenty to thirty cases. Cocoonless cells were found to possess hibernating larvae, pupae, and emerging adults and there was no indication that such a condition was detrimental to the bees. The cause of it is unknown.

Upon completion of feeding and before cocoon construction begins, the larva commences to defecate. The excrement is composed primarily of pollen grains whose surfaces are visibly unaltered. Two patterns of defecation were encountered depending upon whether or not a cocoon is eventually produced. In either case, the feces are at first appressed to the cell wall as elongate flattened pellets which in general parallel the long axis of the cell. This material is applied more or less evenly to all surfaces of the cell and is encountered even on the inner face of the plug. However, it is never sufficiently copious to coat more than an estimated 35 percent of the total interior surface.

If a cocoon is to be spun, silk production then commences and the remainder of the feces are incorporated in the cocoon. As indicated above, there is an abundance of fecal material matted with the silk in a "normal" situation. It imparts a brownish color to the surface and accounts for the rigidity of the finished case. Like the excrement applied to the cell wall, it is deposited in a longitudinal direction. Consequently faint wrinkling of the surface of an unearthed cocoon follows the longitudinal paths of weakness, and similarly directed light streaks can be detected where little or no fecal material has been deposited.

If a cocoon is not constructed, the remainder of the feces is plastered at least usually in a mass to the posterior end of the cell. The situation is not known when only a very little silk is spun.

The cocoon itself does not adhere strongly to the cell surface but may usually be removed intact from a half exposed cell. Compared with its external surface, the internal one is usually similar in color and appearance except slightly shinier.

A microscopic examination of a cocoon which possessed little fecal material revealed that, while much of the cocoon was composed of thread-like strands of silk, many broad, clear, faintly striated ribbons had also been employed. There seems to be no question but that both are the same secretion molded differently, for found in this cocoon were some thread-like fibers which broadened along their length into ribbons. Furthermore, while one larva was producing silk in the laboratory, we pulled the emerging frazzled strand with forceps and found that it came forth thread-like, being circular in cross section. However, the larva, apparently by momentarily compressing the lips of the salivary opening, was able to flatten the strand, in this case imparting a crimped appearance.

When the ribbons are placed one on top of another, a microscopically rugulose appearance reflecting a glossy shine was produced on the surface of the cocoon. Examination of a "normal" feces-laden cocoon revealed this same texture present on the inner surface. It was not as noticeable, however, on the outer, a fact suggesting that the ribbon type secretion is not employed there to the same extent.

It should be mentioned that in the laboratory no larva was able to produce a cocoon nor to plaster its feces against the container (wax-lined depression in sand). The silk which was produced appeared as frazzled fibers and the feces merely fell as elongate pellets.

After the cocoon is completed, the hibernating stage commences. The position of the larva is that of a loop with the labium nearly touching the eighth abdominal sternum. Although some exceptions have been uncovered, the curved midsection of the larva usually lies closest to the anterior end of the cell, while the adjacent anterior and posterior extremes point toward the posterior end. Physiologically, the hibernating larva, unlike the predefecating one, is totally quiescent and not adversely affected by relatively slight changes in temperature.

Pupation probably occurs early in the summer of the following year and unquestionably the pupal period lasts for a relatively short time, compared with the duration of the larval stadium. After the adult has cast off the pupal exuviae and is fully developed, exit is made through the cocoon. Since shreds of matted silk and fecal material have been recovered (along with the pupal skin) from the posterior end of the vacated case, it is assumed that the bee scrapes the anterior end of the cocoon with its mandibles. The exit hole is circular and large, equal in diameter to the tunnel.

In the process of digging its way through the

plug and adjoining tunnel, the bee deposits to its rear so much soil that the cocoon is filled. Over a period of time this soil becomes compact and as a consequence a cocoon from an earlier generation can be removed as a hardened pellet. When no cocoon is produced, the soil forms an internal mold, and, because of the cell lining and large amount of fecal material on the wall, may be freed more or less intact from the partly exposed cell.

During the course of excavation, very few parasites were encountered. A single adult mutillid was seen running through the crevices, but no immature stages of the wasp were found. A number of fully developed larvae of meloids were unearthed. These were large in size and, if parasitic on *Exomalopsis*, it must be assumed that a single individual devoured a number of host larvae. Because of the position of the burrow openings, it is doubtful that bombylid flies could successfully oviposite in them.

CYCLE OF ADULT ACTIVITY

E. chionura appears to undergo but one generation a year, as indicated both by the unearthing of so many hibernating larvae and by the relatively short duration of adult life. The earliest known collection of the species is July 12. The site itself was discovered July 31 and was at this time well populated with adults. Their activity was much reduced by September 1 and none were flying on September 29.

Fragmentary observations suggest that the bees become active above the ground only late in the morning. On August 12, many individuals, both males and females, were flying about and mating at 11:15 a.m., although no pollen-laden females were yet present. The first female bearing pollen appeared an hour later and by 12:45 p.m. many were observed. On both August 20 and September 1 very few bees were flying at 11:00 am. but later both males and females became numerous. Females were seen returning with pollen by 11:10 on the latter day.

PREMATING AND MATING BEHAVIOR

Although considerable time was expended in an attempt to gain an understanding of the premating and mating behavior of these bees, our knowledge of this phase of their biology is incomplete, primarily because of the complexities of the behavior pattern. Most of the available information results from observations at the nesting site. Here numerous individuals of both sexes were seen in swift, though erratic, flight which led them no higher than the surrounding plants (8 to 10 inches). Although most of their time was spent in the air, they frequently landed for brief periods. They alighted in an abrupt "dropping" fashion and seemed to exhibit no preference as to site on which to rest: grass, stones, or ground appearing to be equally suitable. Food for the males was derived at least in part from the yellow composite, which they occasionally visited, although *Lessingia remulosa* var. *micradenia* also may have served as a source.

Many encounters of the two sexes were seen. Sometimes before contacting each other, the male followed a short distance behind the female in flight. Interception may occur when she is either flying or at "rest," but, if the former, the couple is forced to the ground. The initial orientation of their bodies to each other is variable, but the male immediately attempts to reorient himself so that he lies over her dorsum, parallels her body, and faces the same direction. Probably much of the buzzing and tumbling which has been observed occurs during this interval. When he finally is mounted, his antennae are flexed backward over his head, his wings are plaited over his dorsum, and his legs tightly encircle the mesosoma of the female. Although it seems probable that actual copulation takes place while the two are in this position, in no instance out of the numerous observed cases was the male seen to copulate when they were poised thus. His metasoma always extended straight backwards, well separated from hers, and often she flexed hers under her mesosoma so that its apex contacted her head. With the male attached in this position, the female may walk over the ground litter, climb grass stems, and produce intermittent tumbling and buzzing actions as if trying to free herself. The longest recorded time for two individuals being so united is one minute, although longer durations must certainly occur. On occasion it has been noticed that, when a female disengages, the male may attempt to follow her.

Only once were a pair seen *in copulo*. In this instance, one (presumably the female) walked along while dragging the male which faced the opposite direction. The only point of contact was their genitalia.

The mating behavior at the pollen-collecting site was not studied at this locality. However, Rozen observed pairs clasping on the flowers of *Grindelia* the previous year. Hence, it is assumed that mating occurs both at the nesting and pollen-collecting sites.

COMPARISON WITH OTHER SPECIES OF EXOMALOPSIS

There is fragmentary biological information available concerning two other species in the genus: *E.* (*Anthophorula*) *torticornis* Cockerell (Hicks, 1936), and *E.* (*Exomalopsis*) *solani* Cockerell (Linsley, MacSwain and Smith, 1954). On the basis of this and what is known about *E.* (*Anthophorula*) *chionura*, it is possible to present a few generalizations. The females of this genus seem to employ two different methods of reaching the level at which they build their cells. One is by the utilization of available passageways such as cracks (*chionura*) and existing burrows of the

previous generations (*chionura*) or other bees (*solani*); the other, by the females using a common nest entrance (*torticornis* and possibly *chionura*). Such habits would seem to be advantageous since *torticornis* and *chionura* were nesting in very hard soil. The burrows excavated by *Exomalopsis* follow a sinuous course at least in the case of *torticornis* and *chionura*, although such a path may be determined by hard inclusions in the soil or by the existence of previously constructed cells and tunnels.

COMPARISON WITH OTHER EXOMALOPSINAE

Several workers have provided accounts of the biology of other members of the Exomalopsinae.[3] Janvier (1926) discussed the habits of "*Exomalopsis*" *caerulea* Friese, the correct generic assignment of which should be "near *Tapinotaspis* or *Tapinotaspoides*," according to Michener (*in litt.*). The following translation omits only the description of the larva.

"*Exomalopsis caerulea* inhabits Araucania, the region of Conception, and further to the south, the dunes of the Pacific and Lake Budi.

"For nesting the individuals of this species assemble in colonies in January on compact ground in the hardened sand of the dunes and in the chalky slopes. They dig cylindrical burrows which descend tortuously to an average depth of 20 centimeters. Frequently, two or three branches advance in various directions (fig. 78). Each belongs to a bee. Particularly in the chalky beds, a single opening gives entry to numerous workers, which nest in the nearly horizontal branches which are adjacent to one another but do not anastomose. Each bee arranges its cells in a linear series at the end of the tunnel facing the entrance and gives them an ovoid form [not jug-shaped as indicated by Linsley *et al.* (1954)]. She varnishes the interior wall with an application of a secretion which she spreads and makes shiny with the dorsal surface of the abdominal segments. She then gathers the provisions of pollen from the flowers of thistle, of *Calceolaria integrifolia* and *ascendens*, from those of *Lobelia* and *Erynigium*, and forms a small ball at the bottom of the cell; towards the end, she also absorbs nectar, with which she copiously moistens the pollen. The egg rests on top of the ball. When the cell is completed, she closes it with a thick clay partition rolled in a spiral from the side of the neck toward the center. The bee removes from the sides of the tunnel, a little in front of the partition, the material of the partition and expands by the same act the second cell.

"There are three to six cells in each branch. Six weeks after nest building, the larvae have consumed their provisions; they remain surrounded by a certain amount of pollen. After some days of rest, they spin a coriacous cocoon and glue their remains [fecal material] against the wall. They have a fusiform, cylindrical body curved in a horse shoe. . . .

"*Mutilla* frequents the colonies of *Exomalopsis* and parasitizes the larvae."

Michener (1954) tells of the nesting habits of *Ancloscelis panamensis* Michener, as follows:

"A group of about 50 nests was found on a slightly sloping ground on Cerro Cobre, January 20, 1946. The nest entrances were partially hidden by grass and were neither closed nor marked by turrets. The holes went down nearly vertically for 6 to 9 centimeters, and each ended in a single cell. The burrows were unlined and the cells perhaps very thinly lined with a wax-like material. In each completed cell was a pollen mass about 3 by 4.5 mm., firm, with a broad concavity along one side in which an egg was laid. Some larvae were nearly grown; other cells contained only a little pollen."

COMPARISON OF THE EXOMALOPSINAE WITH OTHER SUBFAMILIES

The paper by Linsley, MacSwain, and Smith (1956) makes possible a comparison of the biology of Exomalopsinae (Exomalopsini, *sensu* Michener)[4] with the Emphorinae, Anthophorinae, and Eucerinae. However, in view of the limited information concerning the Exomalopsinae the following must be considered tentative. For purposes of uniformity, we have adopted for the most part the points of comparison and sequence of presentation employed by Linsley, MacSwain and Smith (*ibid.*).

Following this discussion, consideration is given to the possibility that the Exomalopsinae may be ancestral to certain of the parasitic Anthophoridae.

Turrets: With the possible exception of the slight indication of excavated soil surrounding several burrow entrances of *E. chionura*, turrets are not known to be manufactured by the Exomalopsinae.

Cells: In the Exomalopsinae the cells are arranged in a linear series and/or singly, this character agreeing with both the Anthophorinae and the Emphorinae. In *Ancyloscelis panamensis* there is apparently but one cell per burrow. Internally the cells are elongate-oval (not known for *Ancyloscelis panamensis*) and possess a thin lining (compared with *Anthophora*), both these

[3] In a recent paper, Janvier (1955) discusses the biology of *Ancyloscelis baeri* Vachal and *A. analis* Vachal. However, according to C. D. Michener (*in litt.*) and J. S. Moure (personal communication), both species are referable to *Diadasia*, and consequently their biology is not dealt with here. Brèthes (1909) has referred to what he considered to be the nests of *Ancyloscelis armatus* Smith. However, it seems evident from the dimensions and the description that the burrows actually are those of *Melitoma euglossoides* Lepeletier and Serville.

[4] Taxa which are regarded as tribes by Michener (1944, 1953) are considered subfamilies here. This is consistent with the practice of Linsley and his associates at the University of California, Berkeley.

conditions being similar to those found in the Eucerinae. At least with *Exomalopsis chionura* the cell wall is built into the excavation but is variable in thickness, and, as a consequence the external shape can not be compared.

Tunnels: Unlike in other known anthophorids, walls are constructed over part, or even most, of the surface of the tunnels, at least in the case of *E. chionura*.

Cell Provisions: With *E. chionura*, and apparently also with *A. panamensis*, the moistened pollen mass is molded into an elongate, somewhat angulate shape. *"E." caerulea* is said to form it into "une boulette" though whether it is spherical or not is in question. Thus the exomalopsines differ from the members of the Emphorinae, Anthophorinae, and Eucerinae except *Eucera* (Linsley, MacSwain and Smith, 1956). There is no indication of a fermented odor in any of the cells as is the case with the Anthophorinae.

Position of Egg: Although not inserted, the egg of *E. chionura* and *"E." caerulea* is placed on top of the provisions, as in the Eucerinae. The position of the egg of *Ancyloscelis panamensis* is indeterminate, but perhaps not actually very different from other exomalopsines.

Larval Feeding: E. chionura agrees with the emphorines in that the larvae of both continually move about the food and possess the same body form, apparently a modification for this habit.

Deposition of Fecal Material: Again the Exomalopsinae are similar to the Emphorinae because the fecal material is deposited over the inner surface of the cell, although not all is so disposed in the case of *E. chionura*. Likewise, the dorsally situated anus is shared by the two groups.

Cocoon: Unlike members of other subfamilies, *E. chionura* usually spins a conspicuous cocoon which is reinforced with fecal material, although some individuals do not produce a cocoon. In other respects the cocoon of this species is similar to that of the emphorine genus *Ptilothrix* except fewer of the ribbon-type threads are employed by the former.

Pollen Preference: In the Exomalopsinae flower constancy seems to depend upon the genus under consideration. Hence, the work of Timberlake (1947) and of Michener (1954) suggests that at least some *Exomalopsis* are polylectic. On the other hand, the related *Ancyloscelis* Latreille as a genus is apparently monolectic on the flowers of *Ipomoea* (Michener, 1954).

Gregarious Nesting Tendency: At least some members of the Exomalopsinae use a common nest entrance and thus differ from the other subfamilies[5] under discussion. In the case of at least *Exomalopsis chionura*, burrows are used by more than one generation, a characteristic shared only with the emphorine genus *Melitoma* (Linsley and MacSwain, personal communication).[6] *E. chionura*, *"E." caerulea* and *A. panamensis* are known to gather in large colonies and are similar in this respect to the Anthophorinae and the emphorine genus *Melitoma*.[6]

Mating Behavior: Unlike known members of other subfamilies, with the exception of *Melitoma* (Linsley and MacSwain, personal communication), *Exomalopsis chionura* mates at the nesting site as well as at the pollen collecting site.[6, 7]

On the basis of these comparisons the relationship of the Exomalopsinae with some of the other subfamilies can be postulated. Although they differ in many respects (turrets, provisions, position of egg, and fecal material in cocoon), it is our opinion that the Emphorinae and Exomalopsinae can be considered comparatively closely related because of cell arrangement, larval feeding, and deposition of fecal material. Much emphasis is placed upon the latter two features because these are associated with pronounced morphological modifications. The exomalopsines share some biological characters with the eucerines. However, these features can not be considered too significant since they are the sort that have arisen more than once in many bee groups or can be considered as primitive (absence of turrets, thin lining to cell, conspicuous cocoon). Furthermore, the dissimilarities between the two groups are many (cell arrangement, cell provisions except in *Eucera*, larval feeding, deposition of feces, fecal material in cocoon, multilayered cocoon, and gregarious nesting habit). It is obvious from the list of comparisons that the anthophorines and exomalopsines are not closely affiliated, having almost no biological features in common.

It has been suggested by Linsley, MacSwain, and Smith (1954) and Michener (1953) that the Exomalopsinae may be closely related to certain of the parasitic groups (Nomadinae, Holcopasitinae, Epeolinae, Ammobatinae, and probably others). With the exception of the habit of nest appropriation exhibited by *Exomalopsis solani*, only one other biological character may be interpreted as being suggestive of a parasitic way of life; that is in respect to the larval feeding movements. In

[5]The emphorine *Diadasia analis* (Vachal) is apparently similar to the Exomalopsinae with respect to this character (Janvier, 1955).

[6]*Exomalopsis chionura* and *Melitoma euglossoides* Lepeletier share the following biological characteristics: gregarious nesting tendency, mating at the nesting site, and use of burrows from previous generations. These features are unknown elsewhere in the Emphorinae. However, an examination of the mature larva of *M. euglossoides* revealed that it does not differ significantly from other emphorines but was markedly distinct from that of *E. chionura*.

[7]It seems likely that mating at the nesting site would be associated with a gregarious nesting tendency, since males could easily find females which are aggregated in a small area.

the case of *Nomada edwardsii* Cresson, Linsley and MacSwain (1956) report that "feeding on the pollen mass progresses with the larva moving around and around . . ." Illustrations of the partly consumed pollen ball being fed upon by *N. edwardsii* show that it is grooved in a manner somewhat similar to that of *Exomalopsis chionura*. However, whether or not this habit as found in *Exomalopsis* can be regarded as homologous with that of *Nomada* is uncertain, for there are different morphological structures in each group to perform the movements. Hence, in *Exomalopsis* the elongate body form and protruding ninth abdominal sternum represent what is supposed to be adaptations for moving, whereas in *Nomada opacella* a trilobed tenth abdominal segment of the first instar (but apparently not in others) seems to help serve the function. However, the first and perhaps later instars (though not the last) of *Exomalopsis chionura* possesses a spiculate body integument and is thus somewhat similar to *N. opacella*, the first and last instars (and unquestionably others) of which possess a muricate or spiculate body integument.

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THE ADULTS AND IMMATURE STAGES OF AEDES PURPUREIPES AITKEN (DIPTERA: CULICIDAE)[1]

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Aedes (*Kompia*) *purpureipes* Aitken, 1941, one of the most unusual and interesting mosquitoes of North America, has been reported to date from a very few collections made in the Cape Region of Baja California, the north-western Mexican mainland and southern Arizona (Aitken, 1941: 83; Ross, 1943; 86, Vargas, 1949: 261; 1950: 65; Murphy, 1953: 236; Richards *et al.* 1956: 14).

In August of 1954 and 1955 this species was found breeding in large numbers in tree holes at Madera Canyon and Patagonia, Santa Cruz County, and at Gardner Canyon, Pima County, all in southeastern Arizona. Since most of the stages of *purpureipes* are inadequately known, they are more fully described and figured here to supplement the recently published Mosquitoes of North America (Carpenter and La Casse, 1955). Belkin's (1953a, b) systems of chaetotaxic nomenclature and presentation of hair branching statistics are used here without change.

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Aedes (Kompia) purpureipes Aitken

1941. *Aedes* (*Kompia*) *purpureipes* Aitken, Pan-Pac. Ent. 17: 81–4. Triunfo, D. S., Baja Calif., Mex.; holotype ♀ [CAS, No. 5155].

1949. *Aedes* (*Ochlerotatus*) *purpureipes*, Vargas, Rev. Inst. Salubr. y Enferm. Trop. 10: 261.

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1956. *Aedes* (*Kompia*) *purpureipes*, Pratt, Mosquito News 16: 7.

DESCRIPTION

FEMALE.—*Wing* about 2.60–3.20 mm. *Proboscis* dark-scaled. *Palpus* about 0.17 proboscis, dark-scaled. *Antenna* with black integument; torus with a dense mesal patch of broad silver scales. *Vertex* with a median light stripe of short broad silver scales anteriorly, becoming broader and with long appressed broadly-lanceo-

late golden scales posteriorly; submedian dark spot of metallic black broad scales; lateral silver patch of broad decumbent scales enclosing a ventro-lateral bare area of black integument on eye margin; vertical and occipital erect forked scales black, a few on submedian dark spot, majority posterior to spot. *Scutum* with yellowish-brown integument; a narrow golden median stripe of appressed narrowly lanceolate scales extending barely to prescutellar space; a broad black submedian stripe of appressed very narrow lanceolate scales extending to scutellum, scales larger caudally; fossa with golden narrow lanceolate scales; supraalar area with narrow line of similar golden scales dorsally which connects with fossal patch, laterad of this a large sparsely dark-scaled area of very narrow lanceolate black scales which weakly attains fossal patch and is bare posteriorly and bordered laterally by golden narrow lanceolate scales from scutal angle to wing base; prescutellar space weakly bordered by broad decumbent silver scales. *Scutellum* with large median patch of broad decumbent silver scales becoming black apically and with sparse narrower black scales on lateral lobes. *Pleuron* sparsely clothed with broad appressed silver scales in isolated compact patches which are roughly arranged in two longitudinal lines as follows: upper line—dorsal surface of *apn*, middle of *ppn* extending to caudal border, *psp* area, *pa* area cephalad of bristles; lower line—*ppl*, across mid *stp*, middle of *me* to upper bristles; a third line might be pictured as—patch on dorsal fore-coxa, small patch on *lstp* below lower bristles together with patch on dorsal mid-coxa, patch on hind coxa; hypostigial and postcoxal scale patches absent; scales of *me* attain lower third; metameron bare; pleural setae mainly golden, some black, present as follows: *apn* 8–12, mesal group very heavy; *ppn* 2–4, heavy, black, along caudal margin; *ppl* 4–8; *ustp* 2–3; *lstp* 1–4; *ume* 9–15; *lme* (absent), *pa* 6–15; *psp* (absent). *Paratergite* bare. *Wing* completely dark-scaled; scales linear on dorsum of R_s, R_{2+3}, R_2 and R_5, narrow on M and distal 1A, broad elsewhere on dorsum; two or three narrow black scales at base of 1A ventrally. *Halter* light-scaled. *Legs* generally purplish-metallic black with yellow and silver scaling as follows: knee spots weak, silver, often absent on fore-legs, never ringing apex of femora, best developed on hind-femur; fore-femur yellow at base and along proximal three-fourths posteriorly, mid- and hind-femur to proximal third posteriorly; remainder of leg black save for knee spots; fore- and mid-tarsal claws toothed, hind claws simple. *Abdomen* largely light metallic black with narrow transverse pale-yellow indefinite basal bands merging with definite lateral silver scale patches, these latter becoming smaller on distal segments; tergite I with black scales in middle, finely setose laterally; laterotergites silver-scaled anteriorly, dark-scaled posteriorly; sternites predominantly yellow proximally, black distally; segment VIII not completely retractile. Specimens examined: 20.

MALE.—Coloration in general as in female, the pleural setae and scale patches reduced in number and extent respectively. *Palpus* about as long as proboscis. *Antenna* with penultimate segment about equal to 5 preceding segments, apical about equal to penultimate. Claws of fore- and mid-tarsi toothed (Fig. 1g), hind claws simple.

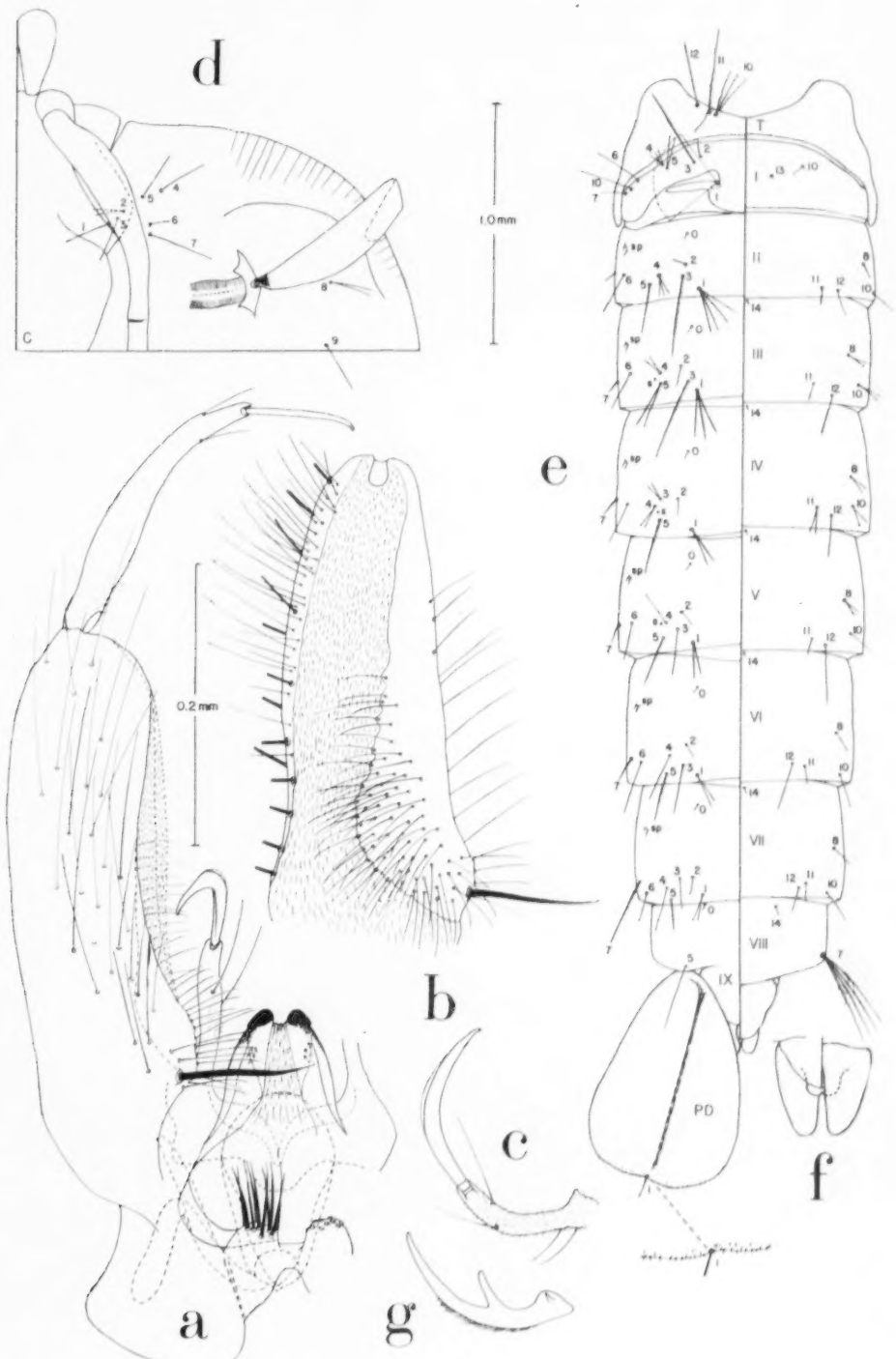
MALE GENITALIA (as in Fig. 1a).—Lobes of ninth tergite well-sclerotized, subquadrate, each bearing many (8–12) strong setae. Proctiger with tenth sternite heavily sclerotized at apical hooks and along sides, with three to six small setae on membrane proximad of hook. Phallosome swollen in apical half, sides well-sclerotized. Claspette stem slender, spiculate to about distal third, bearing two slender setae on mesal margin (seen from dorsal aspect) beyond middle, with more distal one dorsad of other. Claspette filament longer than stem, sickle-shaped, expanded by thin ridge along curvature. Sidepiece (basistyle) four to five times median width, subconical in mesal aspect; with few short setae at base becoming longer, more numerous and mixed with scales distally; basal lobe poorly developed, bearing a heavy differentiated seta on dorsal surface, ventrad an extensive patch of short subequal setae which usually ends on membrane margin at about middle of sidepiece; a few short setae sometimes attaining dorsal margin of membrane in distal fourth; dorsal margin of membrane uneven, ventral margin smoother; apical lobe completely absent. Clasper (dististyle) with claw about half as long as sidepiece, swollen before middle, spiculate in proximal third, bearing two small setae subapically; claw about one-third as long as clasper, slender, apex blunt and curved. Specimens examined: 20.

PUPA.—Linear measurements (in *mm.*; mean and observed range): Abdomen: ♂ 3.39 (3.15–3.70), ♀ 3.86 (3.55–4.15). Trumpet: ♂ 0.51 (0.46–0.55), ♀ 0.56 (0.50–0.65). Paddle: ♂ 0.84 (0.80–0.90), ♀ 0.88 (0.80–0.90). Specimens studied: Above measurements—10♂, 10♀; below description—5♂, 5♀.

Cephalothorax (Fig. 1d, e): Lightly pigmented,

EXPLANATION OF FIGURES

FIG. 1.—Male and pupa of *Aedes purpureipes* Aitken; Santa Rita Mts., Ariz. (UCLA 171–1). a, Dorsal (morphologically) aspect of male genitalia, large lateral setae and scales of sidepiece not shown. b, Mesal aspect of left (morphologically) sidepiece, scales not shown. c, Mesal aspect of left claspette. d, Ventral aspect of left anterior portion of cephalothorax of female pupa. e, Dorsal (left) and ventral (right) aspects of metanotum and abdomen of female pupa. f, Dorsal (left) and ventral (right) aspects of segment IX–X of male pupa. g, Lateral aspect of male mesothoracic claw.


d
1.0 mm
e
0.2 mm
b
a
c
g
f
PD

darker between trumpets and on metanotum. Trumpet darkly pigmented, especially in area of tracheoid; shape variable, usually broadly subconical to distal fourth, then tapered to subquadrate apex; pinna in distal fourth, slit lacking; median reticulations very distinct, shinglelike becoming larger and fainter toward apex. Relative position, length and degree of development of hairs as figured. Hair 1(1), 2(2, 1; 1.67; 1–2), 3(1; 1.05; 1–2), 4(1), 5(1; 1.25; 1–3), 6(1, 2; 1.40; 1–3), 7(1, 2; 1.30; 1–2), 8(2, 3; 2.63; 2–5), 9(1), 10(3, 4, 2; 3.20; 2–6), 11(1; 1.22; 1–4), 12(1; 1.26; 1–3). An anomalous hair is occasionally seen on the mesal surface of the wing case on one or both sides, as in *Aedes* (*Ochlerotatus*) ***muelleri*** Dyar, 1920 and *Aedes* (*Ochlerotatus*) ***monticola*** Belkin and McDonald (1957). Another hair appears sporadically between 8– and 9–C.

Abdomen (Fig. 1e): Moderately pigmented, II–III rather uniform, IV–VIII progressively lighter distally; paddle much ligher than abdomen; II–V usually with two parallel diagonal bars laterally, which fuse on VI and VII and become less distinct on VIII. Rudimentary spiracles of II–VII large, sclerotized; that of I large, usually covered by metanotum in mounted skins. Dorsal sensilla present on III–V. Segment I: reticulations between float hairs small, usually distinct, becoming larger anteriorly; hair 1(50–75 branches), 2(1), 3(1), 4(3, 2–4; 3.26; 2–6), 5(2; 2.00; 1–4), 6(1; 1.16; 1–4), 7(1, 2; 1.40; 1–2), 10(1; 1.20; 1–3). Ventrally an anomalous hair (1, 2; 1.27; 1–5) and a peglike seta are often present. They are here considered homologous to larval hairs 10 and 13 respectively, since hair 11 is lacking in the larva and what is taken to be hair 12 occurs rarely in *Aedes monticola*. This peg (13) and hair (10) are to be seen in certain nearctic *Culex* (*Neoculex*) and may occur in some other genera. Segment II: hair 0(1), 1(4–3, 5; 3.65; 2–5), 2(1), 3(1), 4(3, 4; 3.20; 2–5), 5(1, 2; 1.45; 1–3), 6(1), 7(1), 8(1, 2; 1.58; 1–3), 10(1), 11(1), 12(1); hairs 11 and/or 12 often absent. Segment III: hair 0(1; 1.10; 1–2), 1(3, 2–4; 3.22; 2–5), 2(1), 3(1), 4(2; 2.16; 2–3), 5(1–2; 1.50; 1–2), 6(1), 7(1), 8(2, 1; 1.68; 1–3), 10(2, 1; 2.06; 1–4), 11(1), 12(1; 1.05; 1–2), 14(1). Segment IV: hair 0(1), 1(2; 2.24; 2–3), 2(1), 3(2, 1; 1.83; 1–3), 4(2, 1; 1.68; 1–2), 5(1; 1.06; 1–2), 6(1; 1.06; 1–2), 7(1), 8(2, 1; 1.75; 1–3), 10(2, 1; 1.62; 1–2), 11(1), 12(1), 14(1). Segment V: hair 0(1; 1.05; 1–2), 1(2, 1; 1.84; 1–3), 2(1), 3(1), 4(1; 1.20; 1–2), 5(1; 1.05; 1–2), 6(1), 7(1; 1.05; 1–2), 8(2; 1.95; 1–3), 10(1; 1.10; 1–2), 11(1), 12(1; 1.11; 1–3), 14(1). Segment VI: hair 0(1; 1.10; 1–2), 1(2; 1.83; 1–2), 2(1), 3(1), 4(1), 5(1; 1.20; 1–2), 6(1), 7(1; 1.05; 1–2), 8(1; 1.25; 1–2), 10(1; 1.10; 1–2), 11(1), 12(1), 14(1; 1.05; 1–2). Segment VII: hair 0(1; 1.05; 1–2), 1(2, 1; 1.60; 1–2), 2(1), 3(1), 4(1), 5(1; 1.25; 1–3), 6(1; 1.15; 1–2), 7(1, 2; 1.63; 1–3), 8(1), 10(1), 11(1), 12(1), 14(1). Segment VIII: hair 0(1), 5(1), 7(4, 6, 3; 4.63; 3–7), 14(1). Paddle: hair 1(1; 1.08; 1–2).

Variation: No outstanding variation in morphological or chaetotaxic features was noticed when comparing skins from Patagonia and Madera Canyon. No skins were obtained from the Gardner Canyon collection.

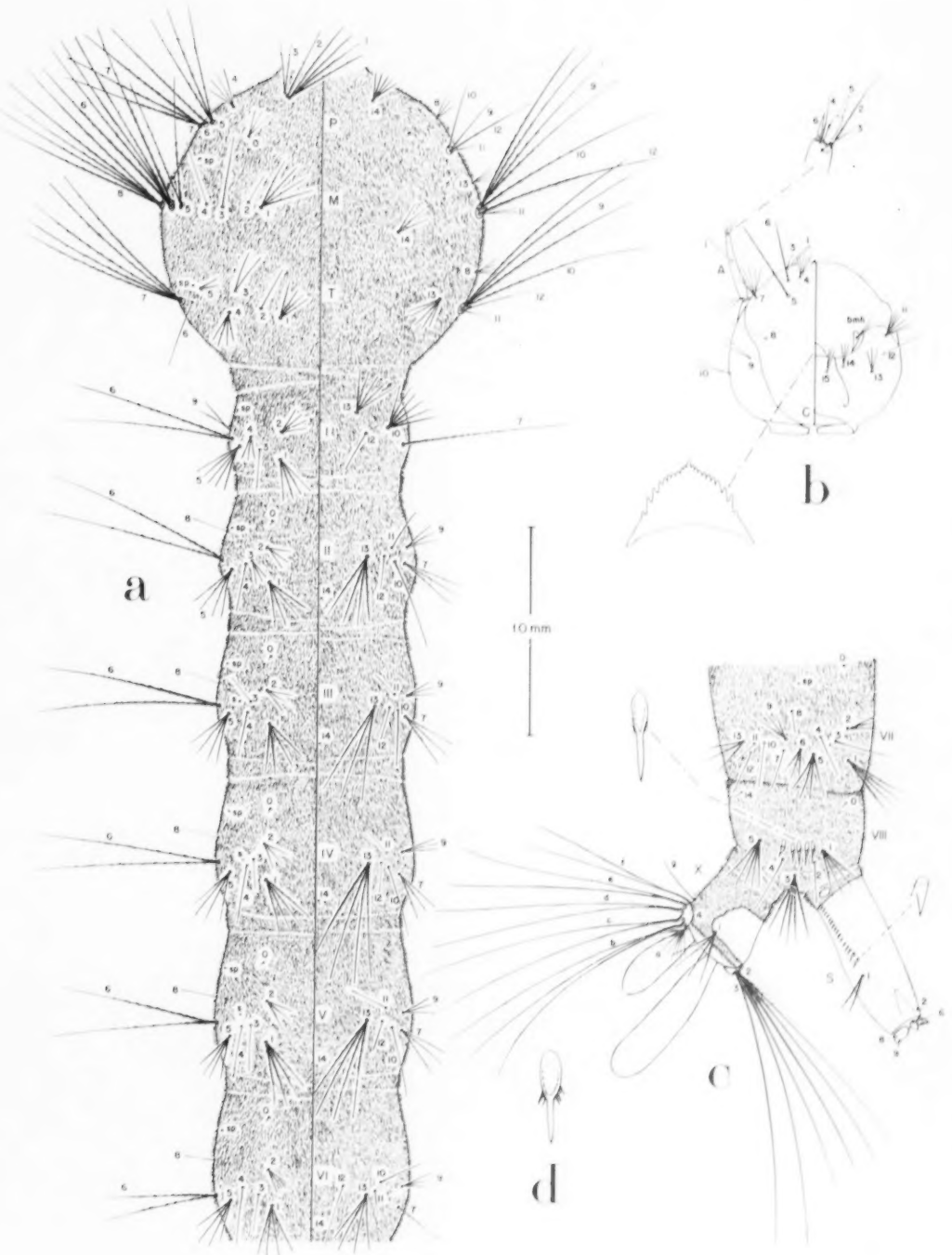
LARVA.—Relative position, length and degree of development of hairs as figured. Specimens examined: 10.

Head (Fig. 2b): About as long (including collar) as wide; maximum width 0.75 to 0.85 mm.; color uniform yellow-brown; integument smooth; collar well developed; width at collar about 0.38 mm. Mental plate as figured, with one strong median tooth and (11, 10; 10.95; 10–12) distinct teeth on each side. Hair 0(1; tiny, slender, ventromesad of hair 3), 1(1; tips bluntly forked in one specimen), 2(not present), 3(1), 4(6, 4–5; 4.74; 3–6), 5(1), 6(1), 7(6, 5; 5.65; 4–8), 8(1), 9(2; 2.00; 1–3), 10(2; 1.75; 1–2), 11(7, 5, 6–8; 6.65; 4–9), 12(1; 1.05; 1–2), 13(3, 4; 3.20; 2–4), 14(3, 2; 2.55; 2–3), 15(3, 2; 2.53; 2–3), basal maxillary hair (fig. 2b, ***bmh***) (3; 3.00; 2–4). Antennal shaft about 0.30 mm. in length, with several minute spicules usually in proximal third and often near apex; hair 1(1) beyond middle; basal sensillum present on proximal margin of sclerotized shaft, giving rise to a 3-branched anomalous hair similar to 11–C in one specimen (UCLA 135–210); apical antennal hairs single.

Thorax (Fig. 2a): Integument thickly long spiculate; rudimentary spiracles on M and T distinct, at positions figured. Hairs 5– to 7–P, 5– to 8–M, 7–T, and pleural groups with sclerotized tubercles; 6, 7–M with common tubercle, tubercles of 5, 6, 7–P confluent or separate; 1– to 3–P and 6–T with small weakly-sclerotized plate near or surrounding alveolus. Prothorax: hair 0(3, 4; 3.95; 3–8), 1(4, 3–5; 4.10; 3–6), 2(1), 3(2; 2.21; 2–3), 4(3–4; 3.72; 3–6), 5(3, 4; 3.21; 2–4), 6(1), 7(3, 4; 3.06; 2–4), 8(3, 4; 3.53; 3–5), 9(1; 1.05; 1–2), 10(1), 11(2; 2.00; 1–3), 12(1; 1.06; 1–2), 14(5, 4; 4.78; 4–6). Mesothorax: hair 1(4, 3–5; 4.00; 3–5), 2(1; 1.10; 1–2), 3(1), 4(1), 5(2; 2.05; 2–3), 6(4, 5; 4.81; 4–6), 7(1), 8(5, 4; 4.95; 4–7), 9(4, 3; 3.89; 3–5), 10(1), 11(2; 2.10; 1–3), 12(1; 1.05; 1–2), 13(4, 3; 3.90; 3–6), 14(3, 2; 2.85; 2–5). Metathorax: hair 1(4; 4.15; 4–5), 2(1), 3(2, 1; 1.85; 1–3), 4(5–4; 4.60; 3–8), 5(2, 3; 2.50; 1–5), 6(1), 7(5–6; 5.50; 5–6), 8(4, 3; 3.95; 3–5), 9(3; 3.16; 3–4), 10(1), 11(2, 3; 2.25; 1–3), 12(1), 13(5–6, 4, 3; 5.15; 3–8).

EXPLANATION OF FIGURES

FIG. 2.—Fourth instar larva of *Aedes purpureipes* Aitken; Santa Rita Mts., Ariz. (UCLA 171-1). a, Dorsal (left) and ventral (right) aspects of thorax and abdominal segments I–VI. b, Dorsal (left) and ventral (right) aspects of head. c, Left lateral aspect of terminal abdominal segments. d, Comb scale; Gardner Canyon, Pima Co., Ariz. (UCLA 136).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Abdomen (Fig. 2a, c): Integument thickly long spiculate; hair 6 with strongly sclerotized tubercle, largest on I, II, disappearing on V or VI; dorsal sensilla present on III to V, at or near positions figured. Segment I: hair 1(4, 5; 4.05; 3–5), 2(4, 5; 4.58; 3–8), 3(1), 4(3, 2; 2.50; 1–3), 5(5, 6, 4; 5.10; 3–7), 6(2), 7(1; 1.05; 1–2), 8(absent), 9(2, 3; 2.55; 2–4), 10(6, 7; 6.40; 5–8), 11(absent), 12(1), 13(5, 4, 6; 5.16; 4–7), 14 (absent). Segment II: hair 0(1, 2; 1.42; 1–2), 1(4; 3.90; 3–4), 2(3; 3.30; 3–5), 3(3, 2; 2.70; 2–3), 4(1), 5(4, 5; 4.65; 4–6), 6(2), 7(3; 3.05; 2–4), 8(1), 9(3; 3.05; 3–4), 10(1), 11(1; 1.05; 1–2), 12(1), 13(4; 4.10; 3–7), 14(absent). Segment III: hair 0(1; 1.25; 1–2), 1(4; 3.89; 3–4), 2(3; 3.10; 3–4), 3(1), 4(1), 5(4, 5; 4.60; 4–6), 6(2; 2.10; 2–4), 7(3; 3.20; 3–4), 8(1), 9(3; 3.10; 3–5), 10(1), 11(1), 12(1), 13(3–4; 3.50; 3–4), 14(1). Segment IV: hair 0(1; 1.05; 1–2), 1(4; 4.06; 4–5), 2(3; 3.05; 3–4), 3(1; 1.05; 1–2), 4(1), 5(4, 5; 4.35; 4–5), 6(2), 7(3; 3.05; 3–4), 8(1; 1.10; 1–2), 9(3; 2.94; 2–3), 10(1), 11(1), 12(1), 13(4, 3; 3.68; 3–4), 14(1). Segment V: hair 0(1; 1.15; 1–2), 1(4; 4.05; 4–5), 2(3; 3.05; 3–4), 3(1, 2; 1.40; 1–2), 4(1), 5(4, 5; 4.35; 4–5), 6(2), 7(3; 2.90; 2–3), 8(1; 1.06;1–2), 9(3; 2.89; 2–3), 10(1), 11(1), 12(1), 13(4; 3.79; 3–4), 14(1). Segment VI: hair 0(1), 1(4; 4.06; 4–5), 2(3; 3.05; 3–4), 3(1), 4(1), 5(4, 5; 4.35; 3–5), 6(2; 2.05; 2–3), 7(1, 2; 1.05; 1–3), 8(1, 2; 1.40; 1–2), 9(3; 2.95; 2–3), 10(1), 11(1), 12(1), 13(4, 3; 3.58; 3–4), 14(1). Segment VII: hair 0(1; 1.13; 1–2), 1(4; 4.00; 3–5), 2(3; 2.95; 2–3), 3(1), 4(1), 5(4, 5; 4.22; 2–5), 6(3, 2; 2.37; 1–3), 7(1), 8(1; 1.16; 1–2), 9(3; 3.16; 3–4), 10(1), 11(1), 12(1), 13(3, 4; 3.35; 3–4), 14(1). Segment VIII: comb scale thorn-shaped with long apical spine and short lateral spinules basally, spine darker than base, its tip usually lighter; scales (5, 6; 5.63; 4–7) in a single straight or slightly curving row; a single specimen has only one scale on the right side of VIII, probably owing to injury in early instar as hair 4 and 5 are absent; alveolus of hair 1–VIII with ventrally-attached, well-sclerotized plate; hair 0(1), 1(4, 5; 4.65; 4–7), 2(1), 3(5, 6, 4–7; 5.50; 4–8), 4(1), 5(5, 4; 4.94; 4–7), 14(1). Siphon: gently convex dorsally, proximal half slightly concave ventrally, extreme apex constricting symmetrically; index (ratio dorsal length to median width) about 2.8 (2.5–3.0); color yellowish-brown, darker on proximal margin and especially at apex; imbrications indistinct; valves well sclerotized; pecten not attaining hair 1–S; teeth (17 to 20; 18.10; 16–21) well aligned, short, individual tooth with one large barb within basal half on leading edge and often one or two smaller proximal teeth; acus free or weakly attached; hair 1–S at about 0.52; hair 1(2, 3; 2.55; 2–5), 2(1), 3(vestige of alveolus shows), 4 and 5 (distinct alveoli), 6(1, surpasses dorsal valve), 7(1, indistinct), 8(1, 2; 1.33; 1–2), 10 to 13 (indistinct, not studied). Segment X: saddle incomplete, reaching about half across segment; pigmentation uniform, similar to that of siphon; imbrications distinct; cephalic and caudal margins simple, ventral margin variably indented, all overlapped by integumentary spiculation; dorsal gill longer than anal segment, 0.3 to 0.5 longer than ventral gill, sides subparallel, rounded apically; hair 1(4, 3; 3.89; 3–5; arising at rounded ventrocaudal angle of saddle, about as long as saddle); dorsal brush: hair 2(4, 5; 4.40; 2–6; arising at anterior angle of well-sclerotized tubercle, often with long barbs at base), 3(2, 1; 1.56; 1–2); ventral brush with well-sclerotized, massive cratal plate: 4a(11; 11–14; directed caudad, short, distinct in appearance from 4b–g), 4b(long; 3, 4; 2.90; 1–4), 4c(long; 2; 2.12; 2–3), 4d(long; ?2), 4e(long; 2), 4f(long; 2; 2.20; 2–3), 4g(short; 2.1; 1.56; 1–3; one or both free of cratal plate).

Variation: A single fourth instar larva was collected in an oak tree hole at Gardner Canyon, Pima County. Its comb scales (fig. 2d) are quite distinct in appearance from those of the sycamore populations at Madera Canyon and Patogonia, and may serve to distinguish this population when further collections can be made.

DISTRIBUTION

MEXICO.—Baja California (Distrito del Sur): *Triunfo*, VII–7–1938, holotype♀[CAS]; *Miraflores*, VII–8–1938, 1♀ paratype; *5 mi. W. San Bartolo*, VII–13–1938, 3♀ paratypes; all foregoing collections made at night (A. E. Michelbacher and E. S. Ross) [CAS, USNM, UCB, ENCB; Aitken, 1941: 83]; *3 mi. S. La Paz*, X–7–1941, 2♀, at light (G. E. Bohart and E. S. Ross) [CAS; Ross, 1943: 86]. Sinaloa: *San Blas*, VIII–1943, 1♂, 5♀, pupae, larvae, tree hole (Macias) [ENCB; Vargas, 1949: 261]. Sonora: *Esperanza*, VIII–1943, 1♂, 5♀, pupae, tree hole (Macias) [ENCB; Vargas, 1950: 65].

ARIZONA.—Santa Cruz County: *Patagonia*, VIII–18–1940, 1♀, biting in daytime (E. S. Ross) [CAS?; Aitken, 1941: 83]; *Sonoita Creek, 4 mi. W. Patagonia*, VIII–24–1954, pupae, larvae; VIII–18–1955, 8♂, 14♀, pupae, larvae; sycamore tree hole (W. A. McDonald) [USNM, BMNH, UCLA]; *Madera Canyon*, VIII–22–24–1954, 8♀, pupae, larvae; VIII–17–1955, 223♂, 416♀, pupae, larvae; sycamore tree hole (W. A. McDonald) [USNM, BMNH, UCD, UCLA, CAS, ENCB, etc.]. Pima County: *Tucson*, VII–27–1932, 1 "specimen", (L. P. Wehrle) [Univ. Ariz.; Murphy, 1953: 236]; *Gardner Canyon*, VIII–24–1954, pupa, larvae, oak tree hole (W. A. McDonald) [UCLA].

Vargas' two records may pertain to a single collection.

Since the Baja California collections of the type material were made south of La Paz it is possible that the populations on the Mexican mainland and in Arizona may be subspecifically distinct. The Cape region of Baja California is noted for isolated populations in a number of animal groups.

BIONOMICS

The only adults collected in the field in 1954 and 1955 were several teneral males and females found resting on the sides of the water-filled sycamore stump at Madera Canyon. No specimens were attracted to a gasoline lantern set up beside the breeding site (air temperature 21.5°C, moon two days old) on the night of August 19, 1955.

Adult females will take blood readily in the laboratory, as early as twelve hours following emergence. Females were fed in shell vials held against the wrist and would also bite through the cheesecloth top of a lantern chimney. When spermathecal dissections showed that mating was not taking place in the lantern chimney, the colony was transferred to a 0.14 cubic meter cage. Unfortunately, all succumbed the following day, possibly because of high temperatures (80°F.) in the laboratory.

Most of the 1954–1955 larvae and pupae were collected in a rot hole atop the still-living stump of the sycamore log which contained, in 1955, a single pupa of *Aedes muelleri* Dyar and several larvae and pupae of *Aedes monticola* Belkin and McDonald. Mixed with *purpureipes* were great numbers of early instar *Orthopodomyia signifera* (Coquillett); all of the former species had emerged as adults before *signifera* began to pupate.

TAXONOMIC DISCUSSION

Aedes purpureipes is unique among known American *Aedes* in consistently lacking postspiracular bristles; minute examination of 50 pinned adults (25 of each sex) and inspection of several slide-mounted specimens reveals no trace of this basic generic character. Chiefly on this character, Aitken (1941) erected for *purpureipes* the subgenus *Kompia*. Vargas (1949: 261),discounting this character, placed *purpureipes* in the subgenus *Ochlerotatus* on the basis of the male genitalia. Dr. G. B. Craig, Jr. has examined a slide-mounted, gravid female from the Arizona population, in which the surface sculpturing of the egg shows fairly well through the abdominal pleural membrane. The following (1956, *in lit.*) is quoted with his permission: "In short, the eggs of *purpureipes* appear to be close to *Stegomyia* and possibly parts of *Finlaya*. They show no resemblance to any of the *Ochlerotatus*, *Aedes*, or *Aedimorphus* which I have examined." Belkin and McDonald (1957) discuss the probable affinities of this species with the *pulchritarsis-varipalpus* group of *Ochlerotatus*, but retain it for the present in *Kompia*. They also provide additions to the keys of Carpenter and La Casse (1955) for the separation of the male genitalia and larva of *purpureipes*.

Southern Arizona is characterized by partially or wholly isolated mountain ranges, and is thus an ideal area for the study of tree hole mosquitoes, restricted as they are by their breeding preference. Even more climatically isolated is the Cape Region of Baja California, the type locality of *purpureipes*. Thorough collecting must be done in both regions, as well as in northwestern Mexico, before we can assemble a clearer picture of the phylogeny of this singular species by combining our knowledge of present-day relationships with what we know of the geologic history of the regions concerned.

Specimens of all stages have been deposited at the U. S. National Museum [USNM], the British Museum (Natural History) [BMNH], the Escuela Nacional de Ciencias Biologicas [ENCB], the California Academy of Sciences [CAS], and the University of California (Berkeley, Davis, Los Angeles) [UCB, UCD, UCLA].

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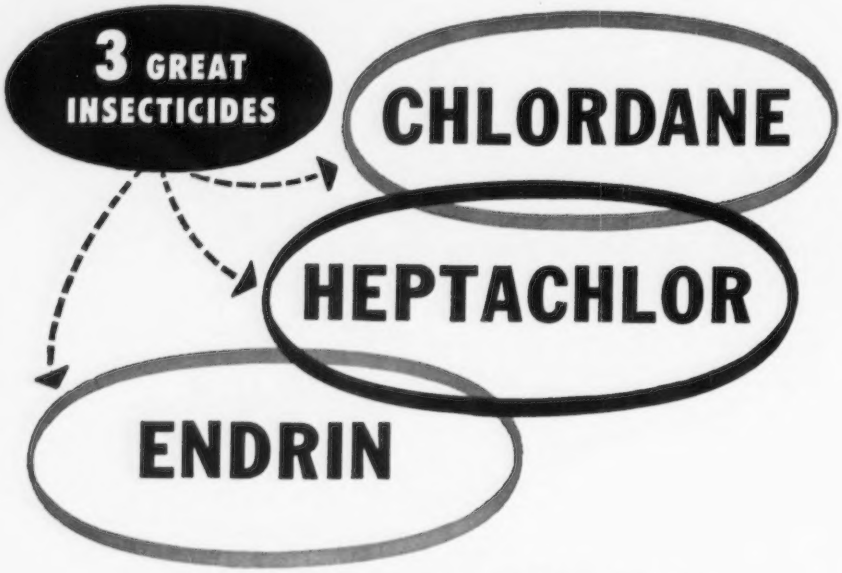

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